HIRTODROSOPHILA OF NORTH AMERICA (DIPTERA: DROSOPHILIDAE)

DAVID A. GRIMALDI



BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

HIRTODROSOPHILA OF NORTH AMERICA (DIPTERA: DROSOPHILIDAE)

DAVID A. GRIMALDI

Division of Invertebrate Zoology

American Museum of Natural History

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY Number 421, 75 pp., 43 figures Issued June 21, 2018

CONTENTS

Abstract
Introduction
Historical Context
Methods and Materials5
Systematics
Genus Hirtodrosophila Duda
Hirtodrosophila alabamensis (Sturtevant)21
Hirtodrosophila chagrinensis (Stalker and Spencer)26
Hirtodrosophila cinerea (Patterson and Wheeler)28
Hirtodrosophila duncani (Sturtevant)29
Hirtodrosophila florida, new species
Hirtodrosophila grisea (Patterson and Wheeler)
Hirtodrosophila jaenikei, new species40
Hirtodrosophila longala (Patterson and Wheeler)
Hirtodrosophila orbospiracula (Patterson and Wheeler)47
Hirtodrosophila ordinaria (Coquillett)49
Hirtodrosophila pictiventris (Duda)55
Hirtodrosophila prognatha (Sturtevant)60
Hirtodrosophila thoracis (Williston)63
Key to Hirtodrosophila Species of America North of Mexico
Acknowledgments
References
Appendix: Photomicrographs of Type Specimens

ABSTRACT

Species concepts are morphologically revised and updated for members of the mycophagous genus Hirtodrosophila Duda that occur in America north of Mexico. Photomicrographs of external features, illustrations of male and female terminalia, and detailed descriptions are provided for 12 species. One species, H. cinerea (Patterson and Wheeler) is known only from the original description; its status is uncertain. Species exclusively from the southwestern United States are H. grisea (Patterson and Wheeler), H. longala (Patterson and Wheeler), and H. orbospiracula (Patterson and Wheeler). Hirtodrosophila alabamensis (Sturtevant) and H. duncani (Sturtevant) are widespread throughout the eastern half of North America; the latter species is morphologically disparate for Hirtodrosophila but provisionally retained in the genus. Hirtodrosophila chagrinensis (Stalker and Spencer) is very rare, known only from two female specimens from the northern United States. Hirtodrosophila ordinaria (Coquillett) is the most widespread species of the genus in North America, occurring throughout the northern half of the continent up to Alaska; H. shaitanensis (Sidorenko) from far eastern Russia may be a junior synonym. A preliminary scheme of relationships in the H. melanderi species group (including H. ordinaria) is presented. Two species from Florida (H. pictiventris [Duda], H. prognatha [Sturtevant]) and one from Florida plus other Gulf states (H. thoracis [Williston]) are widespread throughout the Caribbean, Central America, and portions of South America. Hirtodrosophila mendeli (Mourão et al.), from Brazil, may be a junior synonym of H. prognatha. Two new species are described from southern Florida: H. florida, n. sp., and H. jaenikei n. sp., the latter in the nigrohalterata species complex. A key to the North American species is provided.

INTRODUCTION

Hirtodrosophila is a cosmopolitan genus of 157 species of flies that congregate on fungi, their greatest diversity being tropical. Throughout the world the preferred hosts appear to be moist, pliant polypores (Polyporaceae: "shelf" or "bracket" fungi), although softer fungi are also used, like gilled *Pleurotus* (Pleurotaceae: Agaricales), the rubbery to gelatinous *Auricularia* (Auriculariaceae: Auriculariales), and even stink horns (Phallaceae). The fungus is a breeding site, where larvae burrow into and ingest the fungal tissue, and the spores and surface yeasts are a source of adult food as well (Buxton, 1960; Burla and Bächli, 1968; Lacy, 1982; Shorrocks and Charlesworth, 1980; 1982).

Species of *Hirtodrosophila* vary greatly in habitus from minute, entirely whitish and light yellowish, to bulky individuals elaborately patterned with brown markings, and species that are almost entirely black. Unlike the closely related genera *Mycodrosophila* and especially *Zygothrica*, the wings are rarely patterned. Because they settle on their fungus hosts, these flies are not typically captured using standard insect-collecting techniques such as sweeping, Malaise traps, or trapping with

fruit baits. They must be collected directly from the fungus. Thus, *Hirtodrosophila* specimens are usually rare in museum collections and the species and geographic sampling is poor.

Hirtodrosophila species in other regions have been described in excellent morphological detail: for northern Europe (Bächli et al, 2004), the Neotropical Region (Vilela and Bächli, 1990, 2004); and Asia (Okada, 1956; Bächli, 1974), in particular. My intention with the present work is to clarify ambiguities that arise in identifying and studying the North American species.

HISTORICAL CONTEXT

The 10 North American species of *Hirtodrosophila* known until now were described piecemeal in seven papers, as specimens of rare and extralimital species became available to nine taxonomists over a period of some 50 years. Almost all the species were originally described in the genus *Drosophila* or in *Hirtodrosophila* after it was classified as a subgenus of *Drosophila*.

The first species identified, *H. thoracis* (Williston), was originally known only from the Caribbean island of St. Vincent, described by

Samuel W. Williston (1852–1918) in his monograph of the flies of that island (Williston, 1896). Williston was a physician, paleontologist, entomologist, and noted professor, and is often considered the first American-born dipterist. His Diptera of St. Vincent (1896) is one of the first major studies of a Neotropical fly fauna.

Daniel W. Coquillett (1856–1911) described the second species in the genus, *H. ordinaria* (Coquillett) from throughout the northern half of North America (Coquillett, 1904). He was an applied entomologist and taxonomist working for the USDA and, as "honorary custodian" of the USNM collection at that time, he described over 1,000 species of flies in 67 families.

One of the most influential early workers on drosophilids was Alfred H. Sturtevant (1891–1970), who described *Hirtodrosophila alabamensis*, *H. duncani*, *H. melanderi* (a synonym of *H. ordinaria* [Lacy, 1981]), and *H. prognatha* (known only from the Caribbean at the time) (Sturtevant, 1916, 1918a, 1918b). He published these and other descriptions while still a graduate student in the famed "Fly Group" of T.H. Morgan at Columbia University, soon thereafter monographing the North American fauna (Sturtevant, 1921).

Contemporaneous with Sturtevant and equally influential was the German physician and amateur dipterist, Oswald Duda, who described H. nigrohalterata and H. pictiventris, from Costa Rica (Duda, 1925), the latter species now known to be very widespread. Duda's work was careful for its time; he published detailed descriptions along with drawings of external terminalia and other microscopic characters, and even photomicrographs of wings (e.g., Duda, 1925). His taxonomic focus was on acalyptrates, especially Chloropidae and Drosophilidae; he monographed drosophilids from Africa, Costa Rica, Indonesia, and Taiwan, working principally with collections from Berlin and Budapest.

Sturtevant continued working on the systematics of drosophilids into the 1950s, mostly assisting new groups of American workers.

One group involved Harrison D. Stalker (1915-1982) and Warren P. Spencer (1898-1969). Like Sturtevant, Stalker was principally a geneticist but also an extraordinarily broad biologist and naturalist. The main contribution by Spencer, who was a professor at the College of Wooster in Ohio, was in taxonomy. In a 1939 letter to Sturtevant, he lamented, "I hope that you and Dobzhansky and Patterson and his crowd leave a few odd sub-species or species still to be collected by the time I get time and money to take a crack at it..." (Kohler, 1994: 140). Spencer actually did have the opportunity to codescribe an "odd" species that very same year, Hirtodrosophila chagrinensis (Stalker and Spencer), still one of the rarest species of drosophilids in North America, which I redescribe in the present paper. He probably was not fully aware in 1939 of how Patterson's group was just getting started.

Sturtevant also assisted and advised in its earlier days the University of Texas (UT) Drosophila group, then led by John T. Patterson. The UT group conducted an enormous amount of collecting, descriptions, karyotyping, mating tests and other studies on drosophilids from approximately 1938 to 1970, particularly on species from southwestern North America, including Mexico (e.g., Patterson, 1943; Patterson and Stone, 1952), and later in the Neotropics. One of the first major taxonomic articles from the group was Patterson and Wheeler (1942), in which 37 North American species of Drosophila and Hirtodrosophila were described, among them H. cinerea (Patterson and Wheeler), H. grisea (Patterson and Wheeler), H. longala (Patterson and Wheeler), and H. orbospiracula (Patterson and Wheeler). Scientific legacies of the UT Drosophila group were many, including a collection of living cultures with hundreds of species, which eventually became the Drosophila Species Center that over the years has relocated to five U.S. universities. Another major legacy of the group involved the graduate students who continued with the research program as faculty at various universities. The most influential of all the students was Marshall R. Wheeler (1917–2010), who coauthored the description of four of the North American *Hirtodrosophila* species. He continued at UT as a professor, as steward to the large collections of living cultures and preserved specimens, and as a world authority on drosophilid systematics.

Despite the history of drosophilid research in the United States, the North American species of *Hirtodrosophila* have been poorly characterized and difficult to identify. This is partly due to the obscurity of *Hirtodrosophila*. By 1942, when all but two of the species were described, the total number of specimens reported in the literature for *Hirtodrosophila* was 35. Sampling has improved since then, but not by much. Three species, for example, are still known from only one or two specimens: *H. chagrinensis*, *H. jaenikei*, n. sp., and *H. orbospiracula*. There are no specimens known for *Hirtodrosophila cinerea*.

The other reason for the poor species characterization is of course the nature of insect systematics in the time of Williston, Coquillett, Sturtevant, and Duda. Ironic, though, is the meticulous effort by the UT Drosophila group in dissecting and illustrating the soft, internal reproductive organs like testes and ovaries and the karyotyping of a great many species, without illustrating the male genitalia. By the 1950s it was well known that the complex sclerotized structures of male genitalia, such as the surstyli, hypandrium, and aedeagus, and even the female terminalia (e.g., oviscapt, spermathecae) are most informative for morphologically separating and identifying species (e.g., Okada, 1956). In fact, Wheeler made thousands of permanent slide mounts of the genitalia of many species (housed in the AMNH), well before he began to illustrate these structures in his publications in the 1960s. The early UT practice may have been based on a perception that the soft internal reproductive organs and chromosomes should be particularly informative in a phylogenetic sense. Regardless of the reason, the omission

of male genitalia from descriptions has greatly complicated identification of the richest archives of specimens, which reside in museums.

The only recent work on North American *Hirtodrosophila* is that of Lacy (1981), who redescribed *H. ordinaria*, provided the first figures of male genitalia, and formally established that *H. melanderi* and *H. magnafumosa* are junior synonyms of *H. ordinaria*. Lacy (1982) provided data on allozyme variation and host use for two eastern species, *H. ordinaria* and *H. duncani*, among other species of mycophagous drosophilids.

I am providing for the first time images of the external morphology, along with descriptions and illustrations of the genitalia for both sexes of most North American species. I am also adding some new geographical and host records, and can confirm that the widespread Neotropical species *H. pictiventris* and *H. thoracis* occur in the United States (as mentioned in the catalog by Wheeler [1981]), based on my comparison of male genitalia to those of specimens throughout their neotropical ranges. What had been thought, however, to be *H. nigrohalterata* in Florida (e.g., Wheeler, 1981) is actually a new species, described here. A striking new species, also from Florida, is presented.

METHODS AND MATERIALS

The specimens used for this study derive from my own fieldwork and that of several others (see Acknowledgments), along with the examination of type and nontype museum specimens. Unless specified the specimens are in the AMNH. Preservation techniques varied from air-drying for the older specimens (which leaves them slightly greasy, faded, and collapsed, making the interpretation of original colors difficult) to critical-point drying (CPD) and drying with the solvent HMDS (hexamethyldisilazane) for more recent ones (which leaves them fully distended, clean, with natural colors well preserved). A drawback with HMDS-dried specimens is that the DNA is probably not preserved. I have tried to base



FIG. 1. Polyporus fungus host of *Drosophila duncani*, in New Jersey. Ten specimens were found amongst an aggregation of several hundred specimens of *Mycodrosophila claytonae* Takada and Wheeler (in center).

descriptions and photomicrographs on well-preserved specimens, though only old, historical specimens were available for some species.

Dissections involved snipping off certain body parts and macerating in very warm (not boiling) 10% KOH for about two hours, then rinsing in water, then 70% ethanol, and disarticulating with fine minutens in glycerin, and then mounting on glass slides using glycerin jelly (gelatin). Sketches involved use of a drawing tube on a compound microscope. Afterward, each dissection was placed in a small drop of glycerine and stored in small capsules pinned below the specimen. Even if kept moist, over years glycerin jelly will become impossible to melt. Dissections in old glycerin jelly are easily removed by soaking in a small well of very warm lactic acid, which will dissolve the old matrix in about an hour. For this project dissections of terminalia (male and female) were

made of 85 specimens; applied to the pin for each is a label with a sequential number, prefixed by NAHD ("North American *Hirtodrosophila*"). For photomicrographs and illustrations I used North American specimens, unless otherwise indicated.

MEASUREMENTS were made on dried, point-mounted specimens (and for some wings, slide mounted) using Nikon NIS Elements* software on an SMZ 1500 stereoscope. Measurements were standard ones used for drosophilids, the protocols described in Bächli et al. (2004) and summarized as follows:

HEAD: CD, cheek depth; CD/ED ratio; ED, greatest length of eye; ED/EW ratio; EW, greatest width of eye; FD, face depth below uppermost margin of ptilinal suture; FD/FW ratio; FL, frontal (frons) length; FW, face width, between lateral margins of ptilinal suture; HD, head depth, from ocellar mound to bottom of cheek; HW, head

width (between outside margins of eyes); HW/HD ratio; IV, length of inner vertical seta; LFW, width of frons above ptilinum; OC, length of ocellar seta; Ocellar S-index, OC/POC; OR1, length of proclinate orbital seta; OR1/OR3 ratio; OR2, length of anterior reclinate orbital seta; OR2/OR1 ratio; OR3, length of posterior reclinate orbital seta; OV, length of outer vertical seta; POC, length of postocellar seta; VT-index, IV/OV.

THORAX AND WING: 4-V index, MIV/MIII; 5X-index, ratio of CuAA/dm-cu; ADC, anterior dorsocentral seta length; AKE, anterior katepisternal seta ("sternopleural") length; CII, costal length between tip of R₁ (or costal break) and tip of R_{2+3} ; CIII, costal length between tip of R_{2+3} and R₄₊₅; CIIIb, length of thick spinules along CIII section; CuAA, length of CuA distal to crossvein dm-cu; DC-index, ADC/PDC; dm-cu, length of this crossvein; MIII, length along M between crossveins; MIV, length along M distal to dm-cu crossvein; PDC, posterior dorsocentral seta length; PKE, posterior katepisternal seta ("sternopleural") length; S-index, AKE/PKE; ThL, thorax length; ThL/WL ratio; WL, wing length; WL/WW ratio; WW, wing width.

The descriptions include just the ratios/indices, with the exception of thorax length (ThL), used here as an index of body size. The number after each ratio/index is the average, followed by the range in parentheses; if there is just one number then there was either just one specimen measured or the value was invariant.

For many of the distribution records mapped out for each species by Patterson (1943), specimens were not retained in the former UT collection, making it difficult to impossible to assess their identifications. I cite such records below in the comments section of the respective species. Those specimens that were retained were usually just representative slide-mounted dissections, which bear numbers corresponding to entries in field notebooks with full data. I have quoted field notes verbatim where I felt it was necessary; otherwise, this information was condensed here.

SYSTEMATICS

Genus Hirtodrosophila Duda

Hirtodrosophila Duda 1923: 41. As subgenus,
 type species Drosophila carinata Duda;
 Grimaldi (1990), elevated to genus.
 Dasydrosophila Duda, 1925: unjustified replacement for Hirtodrosophila.

DIAGNOSIS: Eye from bare to having short, dense pilosity; anterior reclinate orbital seta small to minute; postocellar setae generally crossing; carina generally very short and narrow, nearly missing in some species; arista almost always with one ventral branch, near apex; basal flagellomere with long fine setulae in some species; cibarium with sclerotized hypopharyngeal bulb, reduced number of medial sensilla (Grimaldi, 1990); oviscapt with simple margin or apical pegs differentiated, spermathecal capsule generally rounded, sclerotized; male: cerci not connected to epandrium; epandrium often with well-developed ventral lobe; surstylus often divided into dorsal and ventral lobes; hypandrium and aedeagus well developed but relatively simple.

Type Species: Hirtodrosophila carinata Duda. COMMENTS: The genus is probably paraphyletic with respect to Mycodrosophila Oldenberg, Paramycodrosophila Duda, and Zygothrica Wiedemann. Each of these particular genera appears to be monophyletic (Grimaldi, 1987; 1990), but may be closely related to certain groups within Hirtodrosophila. There are some groups within Hirtodrosophila that appear to be monophyletic, such as the H. hirticornis group (defined by the large, projecting pegs at the apex of the oviscapt). If this is the case, there may need to be a division of some Hirtodrosophila into these other genera, with a more narrowly defined *Hirtodrosophila* (sensu stricto) for some. Any reclassification should ideally involve a revision of the world species as well as further phylogenetic study using morphological and molecular data.

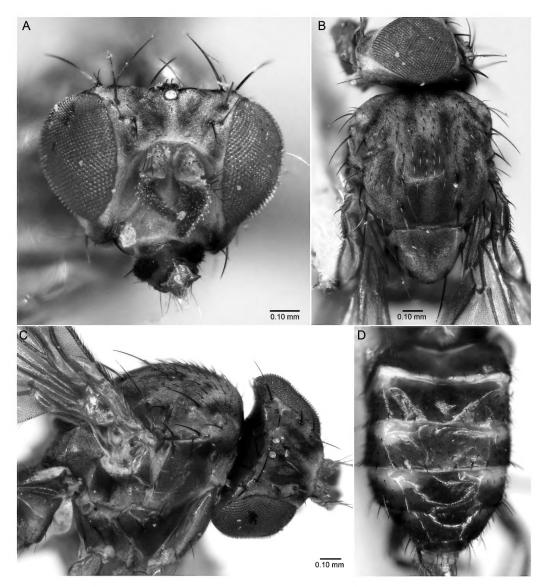


FIG. 2. *Hirtodrosophila alabamensis*. **A.** Head, frontal (male). **B.** Thorax, dorsal (male). **C.** Head and thorax, lateral (male). **D.** Abdomen, dorsal (female).

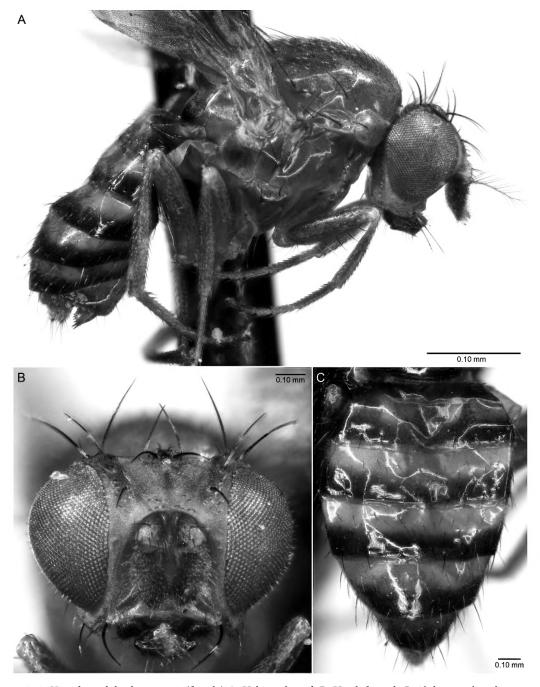


FIG. 3. Hirtodrosophila chagrinensis (female) A. Habitus, lateral. B. Head, frontal. C. Abdomen, dorsal.

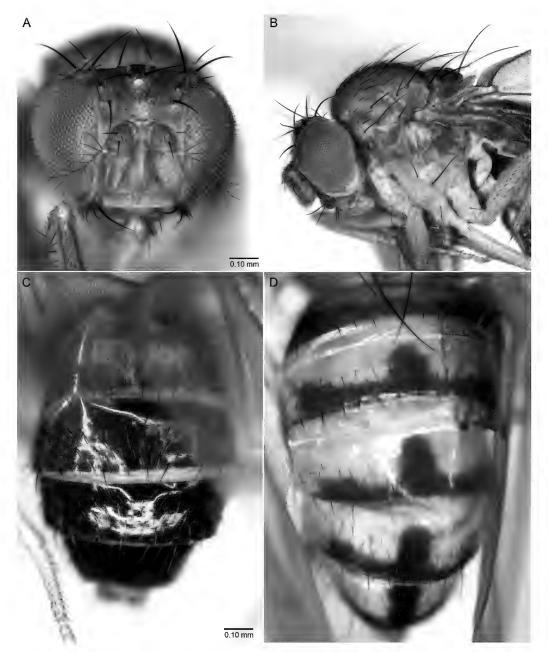


FIG. 4. *Hirtodrosophila duncani*. **A.** Head, frontal (male). **B.** Thorax and head, lateral (male). **C.** Male abdomen, dorsal. **D.** Female abdomen, dorsal.

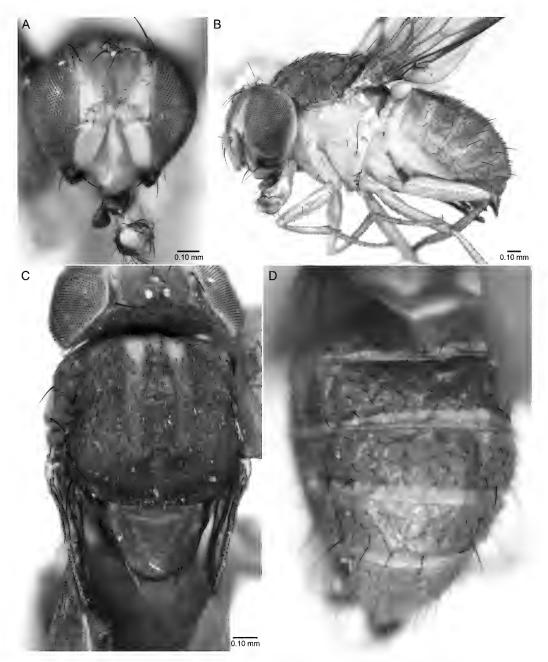


FIG. 5. *Hirtodrosophila florida*, new species (female). **A.** Head, frontal. **B.** Habitus, lateral. **C.** Thorax, dorsal. **D.** Abdomen, dorsal.

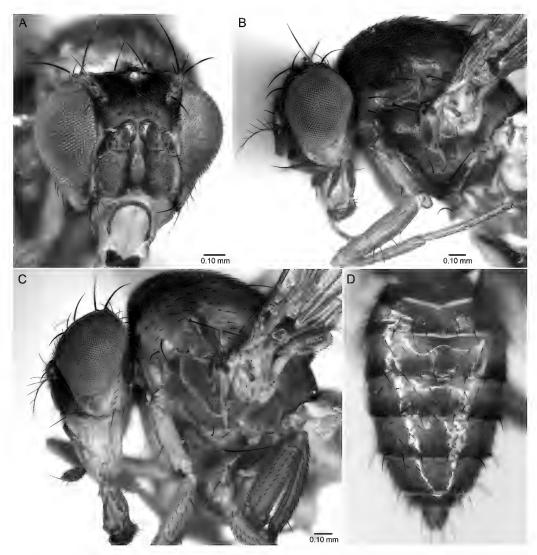


FIG. 6. *Hirtodrosophila grisea*, with some variation in thoracic coloration (B, C). **A.** Head, frontal. **B.** Head and thorax, lateral (male). **C.** Head and thorax, lateral (male). **D.** Abdomen, dorsal (female).

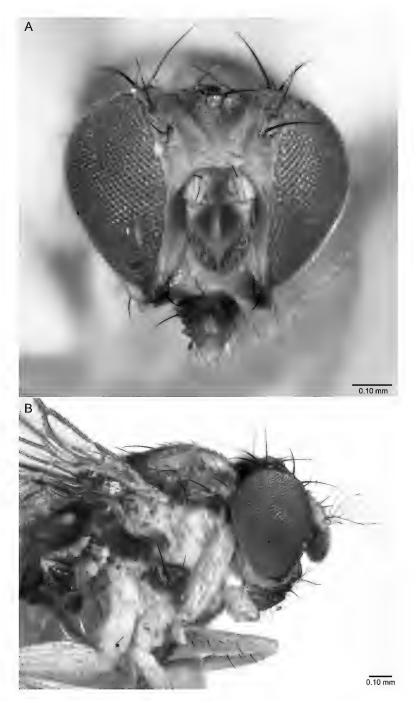


FIG. 7. Hirtodrosophila jaenikei, new species (male holotype). A. Head, frontal. B. Head and thorax, lateral.

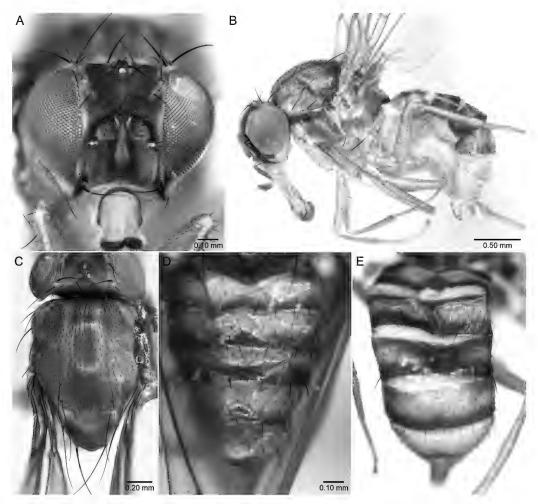


FIG. 8. *Hirtodrosophila longala*. **A.** Head, frontal (male). **B.** Habitus, lateral (female). **C.** Thorax, dorsal (male). **D.** Abdomen, dorsal (male). **E.** Abdomen, dorsal (female).

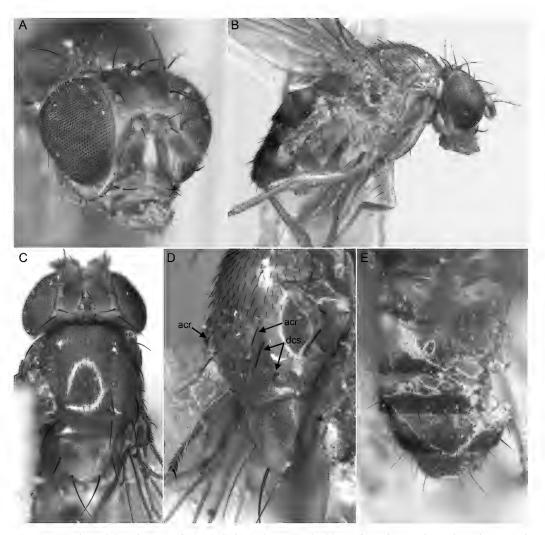


FIG. 9. *Hirtodrosophila orbospiracula* (male holotype). **A.** Head, oblique frontal. **B.** Habitus, lateral. **C.** Head and thorax, dorsal. **D.** Thorax, oblique dorsal, showing enlarged acrostichals anterior to dorsocentrals. **E.** Abdomen, dorsal.

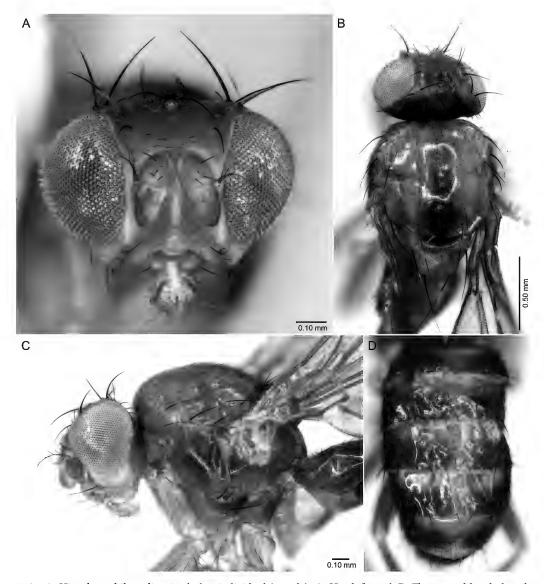


FIG. 10. *Hirtodrosophila ordinaria*, darker individual (a male). **A.** Head, frontal. **B.** Thorax and head, dorsal. **C.** Head and thorax, lateral. **D.** Abdomen, dorsal.

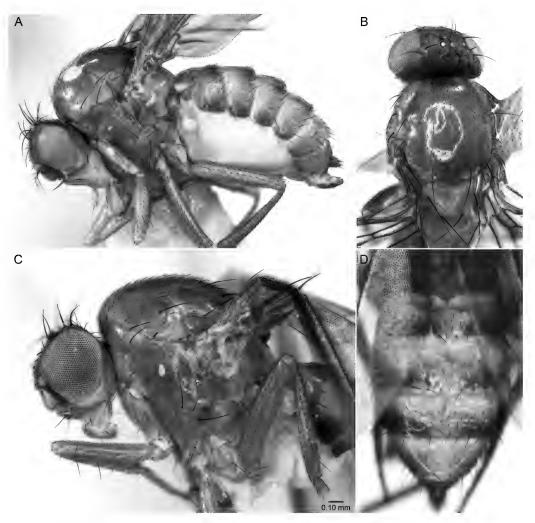


FIG. 11. *Hirtodrosophila ordinaria*, lighter individual (a female). **A.** Habitus, lateral. **B.** Head and thorax, dorsal. **C.** Head and thorax, lateral. **D.** Abdomen, dorsal.

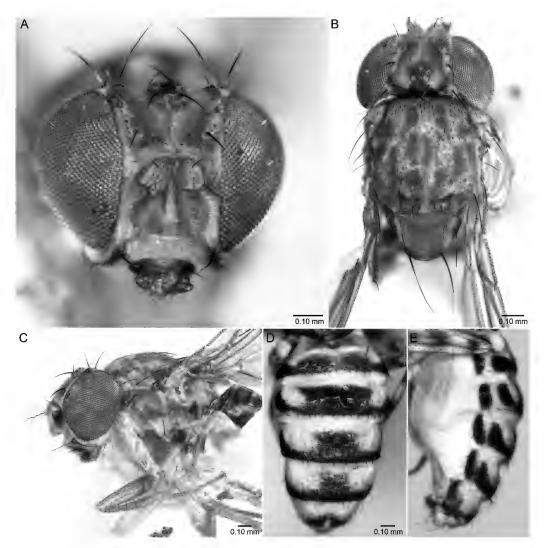


FIG. 12. *Hirtodrosophila pictiventris* (male). **A.** Head, frontal. **B.** Head and thorax, dorsal. **C.** Head and thorax, lateral. **D.** Abdomen, dorsal. **E.** Abdomen, lateral.

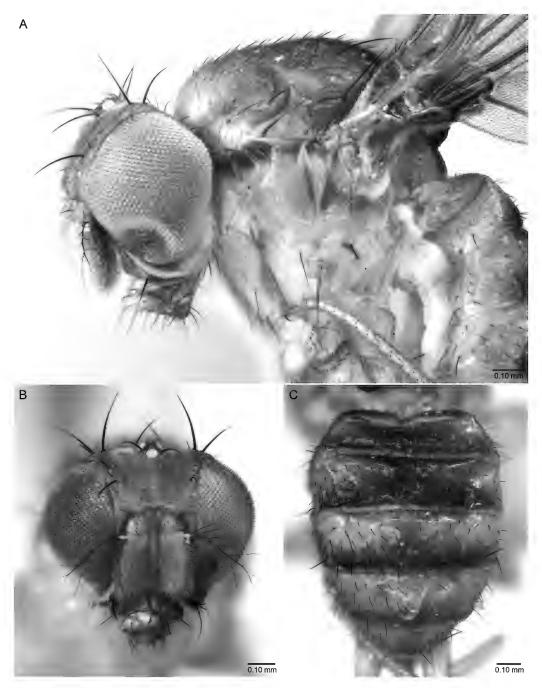


FIG. 13. Hirtodrosophila prognatha (male) A. Head and thorax, lateral. B. Head, frontal. C. Abdomen, dorsal.

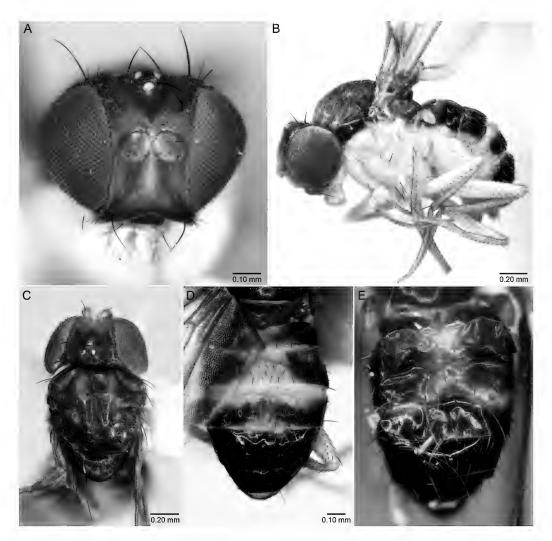


FIG. 14. *Hirtodrosophila thoracis*, showing some variation in abdominal coloration (D, E). **A.** Head, frontal (male). **B.** Habitus, lateral (female). **C.** Head and thorax (male), dorsal. **D.** Abdomen, dorsal (male). **E.** Abdomen, dorsal (male).

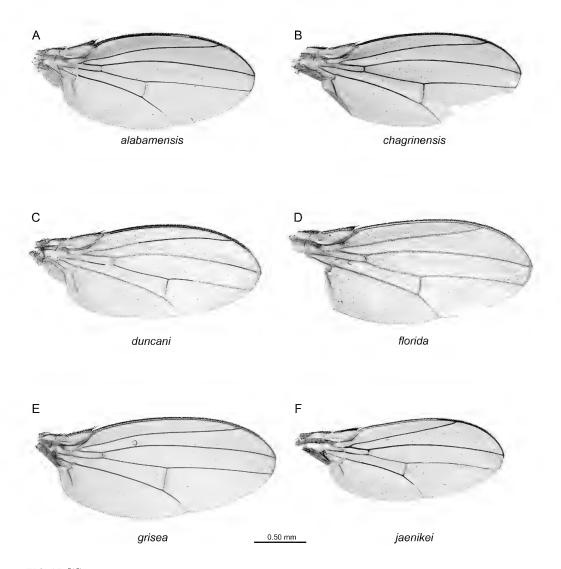


FIG. 15. Wings.

Hirtodrosophila alabamensis (Sturtevant)

Figures 2, 15A, 17, 18, 39

Drosophila alabamensis Sturtevant, 1918a: 38.

DIAGNOSIS: Dark grayish-brown, pollinose fly with faint stripes on scutum; pleuron dark brown with diffuse, light, longitudinal stripe through middle; coloration not sexually dimorphic. Anterior reclinate seta lateral to slightly anterolateral to proclinate; cheek relatively deep (CD/ED 0.25); basal flagellomere without long setulae; wing long (ThL/WL 0.40), slightly dusky, with minute costal lappet at apex of Sc cell; abdomen mostly dark brown with some faint markings. Female: oviscapt heavily sclerotized, unique among North American species, with three posterodorsal pegs on

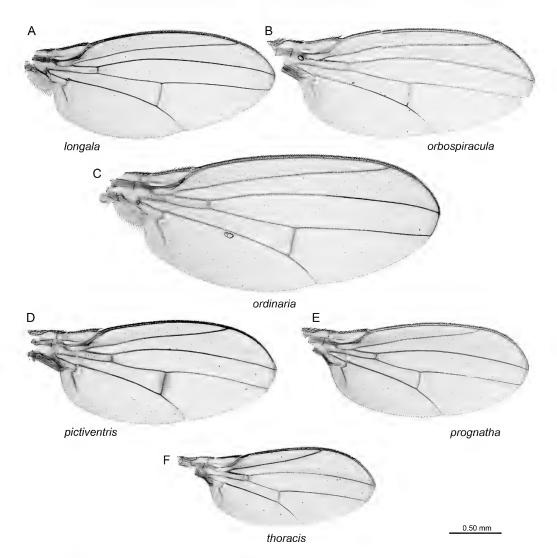


FIG. 16. Wings.

peduncles. Male: hypandrium nearly square; aedeagus short, bulbous, scaled, sclerotized.

DESCRIPTION: Coloration: Little or no sexual dimorphism. Head mostly dull gray with some light areas; ocellar triangle and frontal vittae velvety black-brown, fronto-orbital plates slightly lighter, dull gray-brown; anterior edge of frons yellowish; cheek mostly light, with brown area around and above vibrissa; face dull yellow-

brown; antennal pedicel and basal flagellomere light brown; clypeus and palps dark brown. Eyes brick red. Thorax dull gray-brown; scutum pollinose, with three complete, faint, lighter stripes (in line with dorsocentrals and in middle), pair of incomplete faint stripes just above notopleuron on posterior part of scutum; rim of scutellum slightly lighter than disk; postpronotal lobe dark yellowish; pleuron mostly dark brown, with

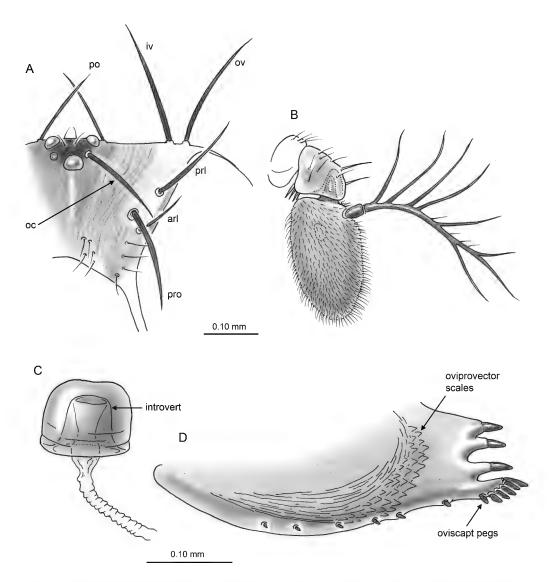


FIG. 17. *Hirtodrosophila alabamensis*, C, D female (dissection no. 79). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca. **D.** Oviscapt, lateral.

diffuse, light, longitudinal stripe in middle running entire length of thorax. Wing slightly dusky, no markings except for small dark spot on veins at Sc break; halter light dusky brown, with darker spots on stem. Legs light dusky brown. Abdomen mostly dark brown, with lighter area on tergite 2 (in middle, triangular),

and on anterolateral portions of tergites 4–6; small light patch on each of tergites 2–5 near lateral margin (decreasing in size caudad). Tergite 8 and proctiger in female slightly lighter.

Head: Frons, face, cheek, scape slightly pollinose. Antenna: Pedicel and scape setose; basal flagellomere with minute, light setulae; arista with

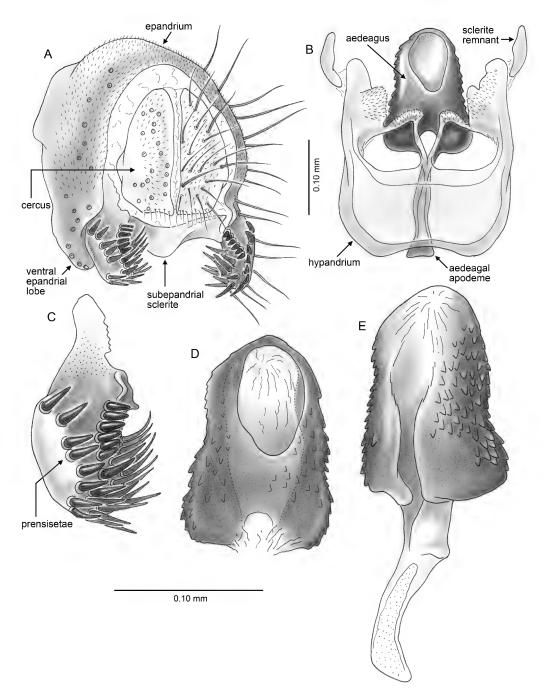


FIG. 18. *Hirtodrosophila alabamensis*, male terminalia (diss. no. 16). **A.** Epandrium. **B.** Hypandrium, aedeagus, aedeagal apodeme. **C.** Right surstylus, posterior view. **D.** Aedeagus, ventral. **E.** Aedeagus and aedeagal apodeme, dorsal.

relatively short branches, 4 dorsal, 1 ventral branch (midway between apical fork and last dorsal branch). Eye shape irregular in lateral view, interfacetal setulae dense and short. Face: slightly concave; carina low, narrow, on upper 2/3 of face. Vibrissa well differentiated, one pair, subvibrissal setae much smaller. Frons: Fronto-orbital plates slightly shiny. Fronto-orbital setae: proclinate approximately same length as posterior reclinate; anterior reclinate about 1/2 the size, directly lateral to slightly anterolateral to proclinate; posterior reclinate slightly closer to proclinate than to verticals. Ocellar seta between anterior and posterior ocelli, approximately same size as proclinate; postocellar setae convergent. Inner vertical seta slightly thicker and shorter than outer vertical. Palp flat, apex rounded; proboscis short, when retracted barely protruding beyond oral margin.

Head measurements (*N* = 4): CD/ED 0.25 (0.16–0.38), ED/EW 1.19 (1.02–1.28), FD/FW 0.99 (0.94–1.06), FL/LFW 0.88 (0.82–0.94), HW/HD 1.46 (1.42–1.50), Ocellar S-index 1.22 (1.11–1.40), OR1/OR3 0.88 (0.80–1.00), OR2/OR1 0.64 (0.63–0.66), VT-index 1.06 (1.04–1.09).

Thorax: Acrostichal setulae in 4-6 irregular rows; acrostichals anterior to dorsocentrals not enlarged. Anterior dorsocentral slightly shorter than posterior dorsocentral. Postpronotum with 2 setae; 3 long notopleural setae, forming triangle; 1 long, 1 short prealar; 1 long supraalar. Anterior scutellars parallel, posterior (apical) scutellars crossing at tips. Anterior katepisternal very short, 0.3× length of posterior katepisternal. Legs: Profemur with ventral row 4 long setae (lengths slightly greater than femur width), lateral row of 4 slightly shorter ones; male protarsus with setulae semi-erect. Mesotibia with ventroapical setae; metatibia with preapical dorsal seta. Wing: C just before Sc break slightly thickened and darkened, Sc break incised, forming minute lappet.

Thorax and wing measurements: 4-V index 2.33 (2.22–2.45), 5-X index 2.84 (2.61–2.93), C-index 2.22 (2.14–2.28), DC-index 0.66 (0.62–0.71), hb-index 1.89 (1.76–2.13), S-index 0.49 (0.48–0.50), ThL 0.96 mm (0.93–1.01), ThL/WL 0.40 (0.39–0.43), WL/WW 2.19 (2.09–2.33).

Male Terminalia: Epandrium taller than wide, with microtrichia overall except ventral lobes; no setae dorsally (lateral surfaces only); ventral lobe of epandrium short, apex not reaching to level of surstylus apex, with lateral row 5-6 setae. Cercus less sclerotized than epandrium; not connected to epandrium; ventral margin flat, with fine setulae, no ventral lobe. Surstylus sclerotized, pendulous, without additional lobe; approximately 30 prensisetae (ca. 13 pegs, including dorsomedial row of 6 pegs, dorsolateral row of 5–6 pegs); thinner, longer prensisetae medially and at apex. Subepandrial sclerite heavily sclerotized, articulating laterally with bases of surstyli, curved in middle. Hypandrium nearly square, with slightly concave anterior margin; postgonites with microtrichia. Aedeagus short, stout, heavily sclerotized, scaled (mostly on lateral and dorsal surfaces). Aedeagal apodeme short, slightly shorter than aedeagus. Female Terminalia: Oviscapt heavily sclerotized, with row of 3 posterodorsal pegs on peduncles; row of apical 6 pegs forming flat, horizontal row beneath pedunculate pegs; row of ca. 6 minute pegs on ventral margin of oviscapt. Oviprovector scaled, but scales relatively small and sparse. Spermatheca heavily sclerotized, dome shaped, introvert extended about 3/4 into length of capsule.

Type: Holotype, female. USA: Alabama, Kushla, IV-9-15, A.H. Sturtevant, Ac. [accession] 5151, holotype, handwritten id label "Drosophila alabamensis Sturtevant." In AMNH. Specimen is missing part of left wing and is somewhat shriveled; not dissected.

Other Specimens Examined: **Canada:** Ontario: Algonquin Park, summer, 1956, D.D. Miller, 13 (dissected, no. 15) (AMNH). USA: Illinois: Carlinville, Marshall R. Wheeler, 9-5-52, 14 (AMNH), Aug. 23, 1954, 14, 13 (dissected, no. 17) (AMNH); Equality, IX/11/52 [no collector), 14, 13 (dissected, no. 16). **Missouri**: Lithium, Je 29, 1955, M.R. Wheeler, 24 (AMNH). **Nebraska**: 3 slides, labelled "D. cinerea -? Nebraska [specific locality not given], male...MW [Marshall R. Wheeler]," one slide of the head, one of the genitalia, a third of the wing, all presumably of the

same specimen. **New York**: Brainard, Rensselaer Co., July 11–22, 1966, P. & B. Wygodzinsky, 1° (AMNH). **Texas**: Austin, Oct. 14, 1950, M.R. Wheeler, 2086.12, 2° (AMNH); Oct. 25, 1950, M.R. Wheeler, 2° (1 dissected, no. 79), 1° (dissected, no. 18) (AMNH); 21 Nov. 1953 M.R. Wheeler, 1° (AMNH). **Virginia**: Montgomery Co., IV/15/52, M. Levitan, 1° (AMNH).

COMMENTS: Male genitalia of the slide-mounted Nebraska specimen unmistakably show the specimen is *H. alabamensis*. Also, see comments under *H. cinerea*.

Hirtodrosophila chagrinensis (Stalker and Spencer)

Figures 3, 15B, 19, 40

Drosophila chagrinensis Stalker and Spencer, 1939: 111.

DIAGNOSIS: Based entirely on female: Head and scutum yellow to orange, latter with faint, slightly darker pair of paramedian stripes; wing yellowish; abdominal tergites shiny, with anterior half dark yellow, posterior half black-brown. Eye with sparse, fine setulae. Oviscapt heavily sclerotized, with vertical row of four posterodorsal pegs above a horizontal, flat row of three apical pegs; spermatheca heavily sclerotized, unique among North American species for large size (ca. 15 µm length vs. usually less than 10 µm) and basal half with five well-defined ribs.

DESCRIPTION: Coloration: Head: Frontal vitta golden bronze, matte, finely striate; ocellar triangle shiny, light outside ocellar boundaries, dark brown within; fronto-orbital plate slightly lighter than frontal vitta, shiny; anterior margin of frons dark yellowish. Antenna: pedicel dark yellow, mesal surface infuscate; basal flagellomere dark brown; arista dark brown, tiny basal articles lighter. Face and cheek cream colored, dark yellow at vibrissal angle; oral margin of face not darkened. Clypeus not exposed in the two specimens; palp dark brown; labellum light brown, rest of proboscis lighter. Eye dull, dark red. Thorax: scutum dull orange, shiny but with light pollinosity, with paramedian pair of faint

darker stripes; scutellum approximately same color as scutum; pleura slightly darker than scutum, particularly under wing. Wing yellowish; legs and halter light. Abdomen: abdominal tergites shiny, with anterior half dark yellow, posterior half black-brown; sternites and cerci yellowish; oviscapt melanized.

Head: Antenna: Scape concealed under ptilinal suture; pedicel with setulae and two larger setae; basal flagellomere relatively short, apex reaching to oral margin (but face is short), arista with four relatively short dorsal branches, one ventral branch (between d4 and apical fork). Eye egg-shaped in lateral view, with sparse, short, fine interfacetal setulae. Face short, concave; carina barely developed, mostly concealed by antennae; one pair vibrissae, subvibrissal setulae minute; cheek of moderate depth. Frons: Frontal vitta finely striate, margins between it and ocellar triangle and fronto-orbital plate well defined; ocellar triangle large, anterior corner extended to level of proclinates. Fronto-orbital setae: proclinate slightly shorter than posterior reclinate seta; anterior reclinate small, fine, ca. 0.3× size of proclinate; posterior reclinate approximately midway between ipsilateral proclinate and inner vertical setae. Ocellar seta long, tip extended past level of proclinate; postocellar setae relatively long, ca. 0.7× size of ocellar, crossed at tips. Inner vertical setae upright, inclinate, approximately same length as outer vertical setae, which are lateroclinate and pointed slightly posteriad.

Head measurements (N=2): CD/ED 0.18 (0.16, 0.20), ED/EW 1.18 (1.16, 1.20), FD/FW 1.09 (1.00, 1.19), FL/LFW 0.85 (0.83, 0.87), HW/HD 1.46 (1.45, 1.48), Ocellar S-index 1.31 (1.30, 1.33), OR1/OR3 0.81 (0.76, 0.86), OR2/OR1 0.39 (0.34, 0.44), VT-index 1.03.

Thorax: Setation: Acrostichal setae in six rows, one acrostichal slightly enlarged just anterior to transverse suture. Anterior dorsocentral ca. 0.7× length of posterior dorsocentral; posterior dorsocentralabout midway between anterior dorsocentral and scutellar margin. Anterior scutellar setae approximately parallel, 0.75× length of posterior scutellar. Postpronotal lobe with 2

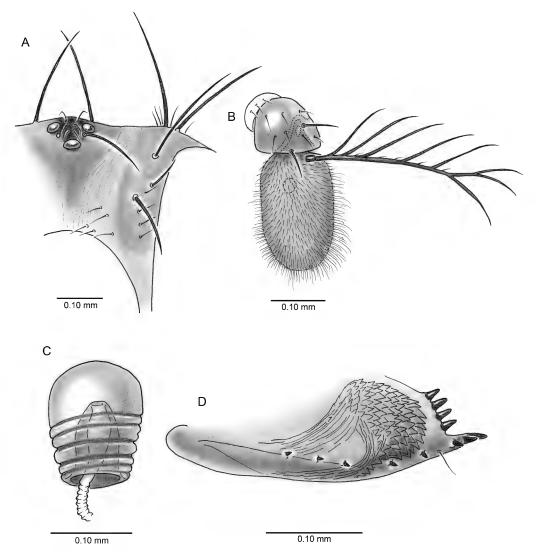


FIG. 19. *Hirtodrosophila chagrinensis*, C, D female (diss. no. 81). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca. **D.** Oviscapt, lateral.

setae; 3 notopleural setae (dorsal one largest, posterior one smallest); anterior supraalar ca. 0.35× length of posterior supraalar; anterior postalar ca. 2× length of posterior postalar; two large katepisternal setae, posterior one larger. **Legs:** Forefemur with ventral row 5 long setae, 2 long lateral setae; no large setae on mid- and

hind femora; male foretarsus unknown; midtibia with large ventroapical seta, hind tibia with small, fine preapical dorsal seta.

Thorax and wing measurements: 4-V index 1.49, 5-X index 1.65, C-index 2.39, DC-index 0.60 (0.59, 0.62), hb-index 2.12, S-index 0.56, ThL 1.17 (1.14, 1.21), ThL/WL 0.45, WL/WW 2.67.

Male Terminalia: Male unknown. Female Terminalia: Oviscapt heavily sclerotized, with vertical row of 4 posterodorsal pegs above a horizontal, flat row of 3 apical pegs, row of 5 minute pegs on ventral margin; oviprovector well developed, fully scaled, scales of moderate size. Spermatheca heavily sclerotized, large (ca. 15 μ m length vs. usually less than 10 μ m), basal half with 5 well-defined ribs, introvert ca. 0.6× length of spermathecal capsule.

Type: Holotype, female. "640, N.[orth] Chagrin, O.[hio], 7/22/37, H.D. Stalker." In USNM. According to Stalker and Spencer (1939: 112), "taken from fleshy fungus in North Chagrin Reservation, Cleveland, Ohio, July 27, 1937 (H.D. Stalker)." North Chagrin Reservation is approximately 15 mi NE of Cleveland.

OTHER SPECIMEN EXAMINED: **USA: Wisconsin:** Mellen, VII/17/52, H.L. Carson, 1° (dissected, no. 81), in AMNH.

COMMENTS: Only two specimens are known to me, the holotype and the specimen cited above from Wisconsin, both females that were examined for this study. The male remains unknown. In the absence of specimens I am unable to confirm the records of *H. chagrinensis* from New York and Michigan cited in several papers (Lacy, 1981; Vilela and Bächli, 2004).

Hirtodrosophila cinerea (Patterson and Wheeler)

Drosophila (Hirtodrosophila) cinerea Patterson and Wheeler, 1942: 71.

DIAGNOSIS: Extracted from description by Patterson and Wheeler (1942): Arista with seven dorsal branches; wing dusky gray, longer than body, with black spot at Sc break; head and thorax largely grayish, with frons and palps darker; scutum with lighter median stripe, bordered laterally by darker gray stripes; pleura with four bluish-gray stripes; legs grayish brown; abdomen yellowish gray, each tergite with complete bluishgray band that widens medially.

DESCRIPTION: See Patterson and Wheeler (1942). Type: Probably nonexistent, but according to the original description: holotype female, Texas: [Sabine County] near Hemphill, "trapped in a fungus patch," August 14, 1940 (Patterson and Wheeler, 1942).

OTHER SPECIMENS EXAMINED: None.

COMMENTS: This is the only North American species for which I did not see specimens. No specimens occur in the AMNH (including the former UT collection) or NMNH, nor does a type specimen exist (it would have been deposited in the AMNH along with the types of H. longala and H. orbospiracula). It is most likely that the type was never deposited and probably lost at the University of Texas. At least for H. grisea, though, there is a dissected, slide-mounted specimen with data that corresponds to the type (see below under grisea). In the former UT slide collection there are three slides labelled "D. cinerea - ? Nebraska male," one of the head, another of the genitalia, and one of the wing. These appear to be from the same specimen, which is actually H. alabamensis (I have labelled it as such). This specimen is probably the basis for subsequent citations (e.g., Vilela and Bächli, 2004). Patterson and Wheeler (1942) mentioned two specimens of H. cinerea in their original description, both from Texas, one from Hemphill (Sabine County, near the Louisiana-Texas border), another from near Austin.

Unfortunately, the original description (Patterson and Wheeler, 1942) is vague and superficial, making interpretation of this species difficult. On the one hand, the description denotes some unique features: a largely gray body with bluish (pollinose) stripes; a long, dusky wing, with "apex of first costal section [apex of Sc cell] black." On the other hand, Hirtodrosophila alabamensis also has these features, though it is not so much gray as it is gray and brown, with pollinose stripes having a slight bluish hue (and configurations not as described for cinerea), and the legs are light, infuscate yellowbrown. Also, the anterior reclinate seta in alabamensis is larger than described for cinerea (ca. $0.5\times$ the size of the proclinate vs. $0.3\times$). Hopefully newly collected specimens will resolve the uncertainty about H. cinerea.

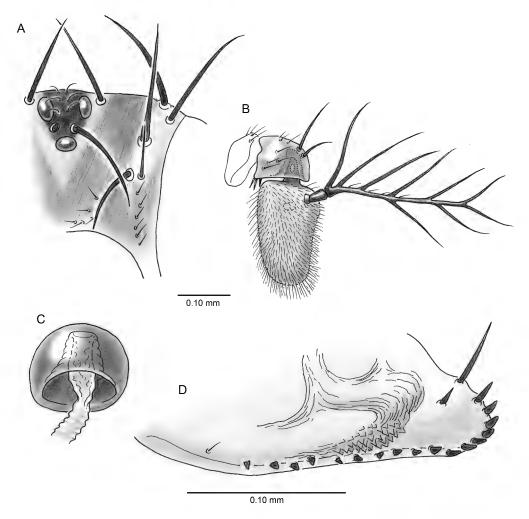


FIG. 20. *Hirtodrosophila duncani*, C, D female (diss. no. 82). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca. **D.** Oviscapt, lateral.

Hirtodrosophila duncani (Sturtevant)

Figures 4, 15C, 20, 21, 41

Drosophila duncani Sturtevant, 1918b: 446.

DIAGNOSIS: Head and dorsal part of thorax largely yellowish ochre, dorsal part of pleura light fuscous brown, ventral part of pleura and legs light cream; abdominal coloration sexually dimorphic (see below); basal flagellomere with long

setulae, arista with two ventral branches; frons relatively narrow (frontal index 0.69), cheek shallow (CD/ED 0.11); crossvein dm-cu close to wing margin; apex of oviscapt unmodified (margin entire); aedeagus short, stout, scaled; paraphyses long, digitate, flanking aedeagus; surstylus bilobed, small inner lobe with marginal row of prensisetae and rows of microtrichia.

DESCRIPTION: **Coloration**: Head: Frons dark yellowish beige, ocellar triangle slightly darker;

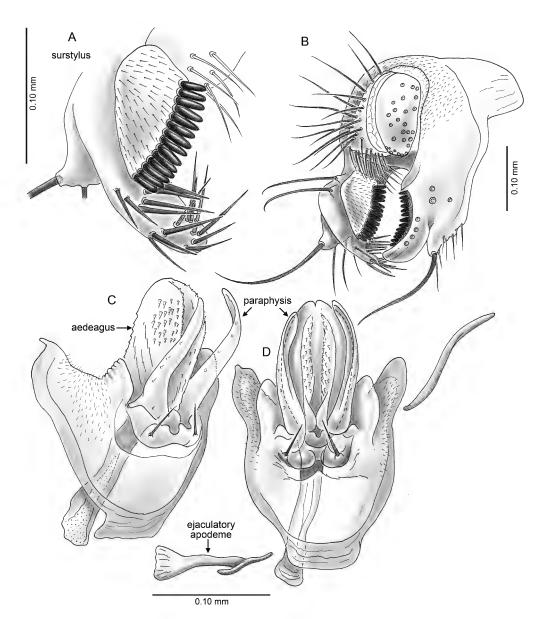


FIG. 21. *Hirtodrosophila duncani*, male terminalia (diss. no. 3). **A.** Surstylus (with microtrichia) with ventral epandrial lobe. **B.** Epandrium and associated structures. **C, D.** Hypandrium, aedeagus, aedeagal apodeme in ventrolateral (C) and ventral (D) views.

fronto-orbital plates slightly lighter than frontal vittae. Face dull yellowish, clypeus and vibrissal angle slightly darker. Palp and proboscis very light. Antenna light, fuscous brown, pedicel slightly darker than basal flagellomere. Eye pink. Thorax: Scutum, scutellum, postnotum deep, dull yellowish to ochre, postpronotal lobe lighter; dorsal portion of pleura light, fuscous brown; katepisternum and meron cream colored. Legs entirely light, cream colored. Wing entirely hyaline, no markings; veins light fuscous brown; halter dull yellow, knob light cream. Abdominal coloration sexually dimorphic: Male with abdomen mostly black brown, shiny; all of tergite 1, anterior half of tergite 2, anteromedian portion of tergite 3 ochre; tergite 3 with median pattern (see figs. 20, 21); tergite 7 remnants and epandrium light, fuscous brown. Female with tergites 2-6 having anterior half light, cream colored, posterior half dark brown; tergites 3-6 with posterior dark band expanded into central spot, spots fused into central, dark median stripe; tergite 1 fuscous brown, tergite 7 (divided medially) dark brown, oviscapt yellow.

Head: Antenna: Scape and pedicel setulose, pedicel with two stout setae on anterior surface; basal flagellomere with long, fine, light setulae, longest ones approximately 1/2 width of flagellomere, apex of flagellomere not quite reaching to level of oral margin; arista with 5 dorsal branches, 2 ventral branches (opposite to dorsal branches 4 and 5, or nearly so), plus small terminal fork. Eye taller than long in lateral view, with dense, light interfacetal setulae. Face relatively flat, with narrow, low carina on upper portion. Vibrissa large, stout, well differentiated; subvibrissal seta approximately half the length of vibrissa. Cheek, clypeus shallow. Proboscis short, largely withdrawn into oral cavity at rest; labellum approximately to length of oral cavity; palp fairly large, bilaterally asymmetrical, with single apical seta. Frons: Of moderate length and width; fronto-orbital plates slightly shiny; frontal vittae dull, finely striate. Fronto-orbital setae well developed: proclinate slightly shorter than posterior reclinate; anterior reclinate directly lateral to

proclinate, approximately 1/2 the size; posterior reclinate noticeably closer to other orbitals than to verticals. Inner vertical seta long, strongly inclinate, outer vertical strongly lateroclinate. Ocellar triangle slightly shiny; ocellar seta nearly reaching to level of ptilinum; postocellar setae convergent but not crossed.

Head measurements (*N* = 3): CD/ED 0.11 (0.09–0.14), ED/EW 1.22 (1.19–1.26), FD/FW 1.06 (1.02–1.12), FL/LFW 0.69 (0.65–0.77), HW/HD 1.34 (1.29–1.39), Ocellar S-index 1.42 (1.23–1.55), OR1/OR3 0.73 (0.62–0.79), OR2/OR1 0.48 (0.41–0.55), VT-index 1.09 (1.08–1.11).

Thorax: Setation: Acrostichal setae in 6 even rows; 2-3 acrostichals immediately anterior to transverse suture slightly enlarged. Anterior dorsocentral ca. 0.7× length of posterior dorsocentral; posterior dorsocentral midway between anterior dorsocentral and anterior margin of scutellum. Anterior scutellar seta slightly smaller than posterior scutellar; anteriors convergent; posterior (apical) scutellar setae crossing at apical third. Postpronotal lobe with 2 small setae; 2 setae very close to notopleural suture (posterior one short); 1 large seta dorsal to these. Two supraalar setae, 1 small postalar. Two large katepisternal setae, anterior one ca. 0.65× size of posterior one; small seta between these. Legs: Forefemur with 2-3 long ventrodistal setae; foretibia with short preapical dorsal seta; ctenidia on tibia and basitarsomere golden, well developed; 2-3 short, black setae at apex of probasitarsomere; male foretarsi without fine, erect setulae on dorsal surface. Midfemur without large setae, midtibia with large, stout ventroapical seta. Hind femur without large setae; hind tibia with small preapical dorsal seta. Wing: Clear, hyaline, no markings; veins light fuscous brown.

Thorax and wing measurements: 4-V index 1.61 (1.60–1.62), 5-X index 1.29 (1.23–1.42), C-index 2.67 (2.42–3.01), DC-index 0.64 (0.62–0.67), hb-index 1.87 (1.70–1.96), S-index 0.57 (0.56, 0.57), ThL 1.11 mm (1.04–1.17), ThL/WL 0.46 (0.44, 0.49), WL/WW 2.23 (2.16–2.32).

Male Terminalia: Epandrium height nearly twice the width and length; with sparse micro-

trichia dorsally, none laterally; anterodorsal phragma large; ventral epandrial lobe small (apex not reaching to level of apex of surstylus), tip of lobe with large, thick, curved seta, much smaller, fine setae anterior to macroseta. Cercus small, not connected to epandrium; with ventral tuft of fine setae; no microtrichia. Surstylus apparently bilobed; with small, inner lobe having inner marginal row of ca. 14 evenly sized prensisetae, inner lobe with microtrichia on outer surface arranged roughly into irregular rows. Apparent outer, large lobe of surstylus ca. 1.5× length of inner one, with ca. 15 stiff, stout setae only on apical half (no prensisetae). Hypandrium roughly U-shaped, with 2 pairs posterior lobes, outer pair with microtrichia. Paraphyses long, digitate, extended to level of aedeagal tip, flattened at tip; with lateral row of 3-4 minute sensilla; pair of short, stout setae near base. Aedeagus short, stout, scaled; slightly shorter than aedeagal apodeme. Flat surface of ejaculatory apodeme oblique to main part of apodeme.

Female Terminalia: Oviscapt with pegs but otherwise unmodified, margin entire, no differentiation of pegs at apex; with ca. 18 pegs along margin, gradually decreased in size anteriad, 1 stout, long preapical dorsal seta. Oviprovector with sparse, small scales. Spermatheca dome shaped, with introvert extended nearly to apex of capsule.

Type: Holotype, female. **USA: Illinois**, Flat Rock, 1915, fungus, ac [AMNH accession] 5300, Type, on handwritten label: "*Drosophila duncani* Sturtevant." In AMNH. Not dissected, in good condition.

OTHER SPECIMENS EXAMINED: **USA: Nebraska**: Crystal Lake Recreation Ground, at 12 mi. S.W. Hastings, 8-22, 23-50, M.R. Wheeler, lot 2069.21, portions of ≥ 4 males (terminalia) on glass slides only (no bodies), which I have labelled A to E, with A, B, D, and E having an epandrium, and C with two mounted hypandria and aedeagi. **New Jersey**: Morris Co., Pompton Plains, VII/23/15 through VIII/12/15, on *Polyporus* fungus, D. Grimaldi coll., $5\ \cdot{\sigma}$, $3\ \cdot{Q}$ (AMNH), $1\ \cdot{Q}$, $1\ \cdot{d}$ dissected (nos. 82, 2, respectively). **New York**: Broome Co., Vestal, VI-15-82, D. Grimaldi,

reared from mushroom *Polyporus squamosus*, $1\,^{\circ}$, $1\,^{\circ}$ (dissected, no. 1). Long Island [Brooklyn], Flatbush, Lost Woods, 8-9-1890, J.L. Zibriskie, $11\,^{\circ}$, $5\,^{\circ}$ ($1\,^{\circ}$ dissected, no. 4) (AMNH). Orange Co., Black Rock Forest [Cornwall], 17/VIII/90, Grimaldi and Stark, on old *Ganoderma tsugae*, $1\,^{\circ}$ (dissected, no. 4).

COMMENTS: This is an intriguing species. It plesiomorphically has two ventral branches on the arista, and the oviscapt has a typical drosophiline structure with an entire margin, rather than the apex modified as in many Hirtodrosophila. Moreover, the hypopharyngeal bulb is not heavily sclerotized as in members of the Zygothrica genus group (which includes Hirtodrosophila) (Grimaldi, 1990), and it has a high number of posterior and medial sensilla on the cibarium (most species in the species group have a highly reduced number). Distinctive apomorphic features include the anterior reclinate orbital lateral to the proclinate; microtrichia in dense rows on the surstylus but sparse on the epandrium and entirely lacking on the cercus; and an apparent bilobed condition of the surstylus, with the inner lobe having a long row of prensisetae and outer lobe with just stiff setae. Lastly, the paraphyses are long, flanking the aedeagus, each with a row of sensilla, similar to what is seen in Scaptodrosophila, Lordiphosa, and some other basal drosophilines, although a few Hirtodrosophila (e.g., kuscheli [Brncic]) have similar paraphyses. Were it not for an egg with four filaments, mycophagy, and the setulose basal flagellomere the position of duncani in Hirtodrosophila would be highly unlikely. It is possible that H. duncani is a very basal species in the genus, but this needs to be tested with molecular data.

Patterson and R.P. Wagner (in Patterson, 1943) listed specimens they examined from Alabama, Arkansas, Mississippi, Ohio, Oklahoma, Tennessee, and Texas, cited by Vilela and Bächli (2004) but which I have not seen. These records may be correct given that this light-bodied species is fairly easy to spot with just external features.

The series of specimens that I collected in Pompton Plains, New Jersey were among a large

aggregation of Mycodrosophila claytonae on a group of pliant, moist Polyporus sp. on a rotting stump (fig. 1). Other host records with specimens include Polyporus squamosus and Ganoderma tsugae (Polyporaceae). Dorsey and Carson (1956) reported a collection of 200 specimens of H. duncani at a site in West Virginia, primarily from traps baited with molasses and vinegar, although some were also collected at traps baited with cultivated fungi. This account may not be very informative of natural habits since Dorsey and Carson collected at the same traps many more Drosophila putrida and D. "transversa" (now known to be D. recens and D. falleni in the eastern United States), despite these being strictly mycophagous species. Hirtodrosophila duncani was rare in the large study by Lacy (1982) of mycophagous drosophilid ecology in northeastern United States. Among the more than 33,000 specimens he reared from various macrofungi in Ithaca, New York, and the Smoky Mountains, Tennessee, 260 specimens were H. duncani (Drosophila falleni, D. neotestacea, and D. putrida greatly predominated).

Hirtodrosophila florida, new species

Figures 5, 15D, 22, 23

DIAGNOSIS: Face and antennae light, cream colored, frons slightly darker but with lateral areas whitish, pollinose; scutum, scutellum, abdominal tergites very light brown; anterior portion of scutum with pair of faint, short, light stripes; pleura, legs, halter entirely light, cream colored. Basal flagellomere with short setulae; head relatively narrow (HW/HD 1.20), frons relatively wide (frontal index 1.11), eve deep (ED/EW 1.56), face deep (FD/FW 1.20); wing relatively short (ThL/WL 0.51). Male: Epandrium dorsally long; cerci large, broad, flat; aedeagus straight, apex with basal flap having fine, irregular serrations. Female: Oviscapt with preapical vertical row of 4 pegs, strongly projecting apical lobe with two large pegs; spermatheca unique, barely sclerotized, slender and fusiform, no introvert, with slight transverse wrinkles.

DESCRIPTION: Coloration: Head mostly light, frons tan in middle, slightly pollinose; fronto-orbital plates lighter, pollinose white; margins of frontal vittae and ocellar triangle barely differentiated; narrow triangle of light brown at base of verticals. Face light, cream colored, including carina, oral margin not darkened; vibrissal angle and anterior portion of cheek beneath eye dark brown. Antenna entirely light, cream colored; branched portion of arista dark. Mouthparts: clypeus and outer surface of labellum light brown, palp darker brown, rest of proboscis light. Eye dull red. Thorax: Scutum and scutellum light brown; scutum with pair of faint, paramedian light stripes anteriorly (between tangents of dorsocentrals), bright spots at anterior end of stripes. Pleura, legs, halter entirely light, cream colored; edge between dark scutum and light pleura at notopleural suture is diffuse, not discrete. Wing hyaline, without markings; apex of C at Sc break slightly darkened, small dark node about midway along Sc. Abdomen with tergites, cerci light brown, lighter than notum; sternites light, cream colored, as for pleural membrane.

Head: Antenna: Scape well exposed, with setulae; pedicel with setulae, 2 larger setae; basal flagellomere relatively long, tip almost reaching oral margin, with short setulae only; arista with 6 long dorsal branches, 1 ventral branch, opposite d6. Eye oblong, tall and narrow in lateral view, with short, dense interfacetal setulae. Face very slightly concave; carina small, narrow, on upper 0.65× of face, oral margin very slightly concave. One pair vibrissae, subvibrissal setulae much smaller. Frons: Fronto-orbital plates, frontal vittae, ocellar triangle matte, margins between them not differentiated. Fronto-orbital setae: proclinate slightly shorter than posterior reclinate; anterior reclinate ca. 0.6× length of proclinate; posterior reclinate slightly closer to proclinate than to verticals; proclinate slightly medial to tangent formed by line through ipsilateral reclinates and inner vertical. Tip of ocellar seta reaching to anterior reclinate; postocellar setae ca. 0.5× length of ocellar, varying from par-

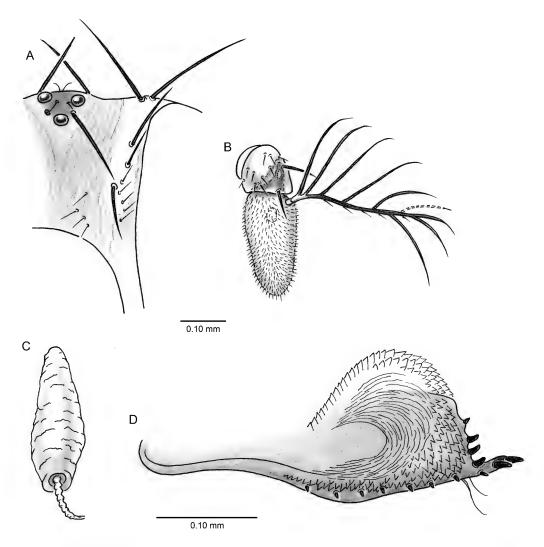


FIG. 22. *Hirtodrosophila florida*, n. sp., C, D female (diss. no. 75). **A.** Frons, portion. **B.** Antenna (dashed branch occurs in some individuals). **C.** Spermatheca. **D.** Oviscapt and oviprovector, lateral.

allel to tips crossed. Inner vertical setae upright, inclinate; outer vertical setae lateroclinate, pointing slightly posteriad; verticals approximately equal in length.

Head measurements (*N* = 2): CD/ED 0.15, ED/EW 1.56 (1.51, 1.61), FD/FW 1.20 (1.13, 1.27), FL/LFW 1.11 (1.03, 1.20), HW/HD 1.20, Ocellar S-index 1.05 (0.93, 1.18), OR2/OR1 0.57, VT-index 1.13.

Thorax: Acrostichal setae in 6 rows; 1 to 2 enlarged acrostichals just anterior to transverse suture. Anterior dorsocentral finer than and ca. 0.8× length of posterior dorsocentral; posterior dorsocentral midway between anterior dorsocentral and scutellar margin. Postpronotal lobe with 2–3 setae; 3 notopleural setae (dorsal one longest); 2 supra-alar setae, anterior one short; 2 postalar setae; katepisternum with one large seta

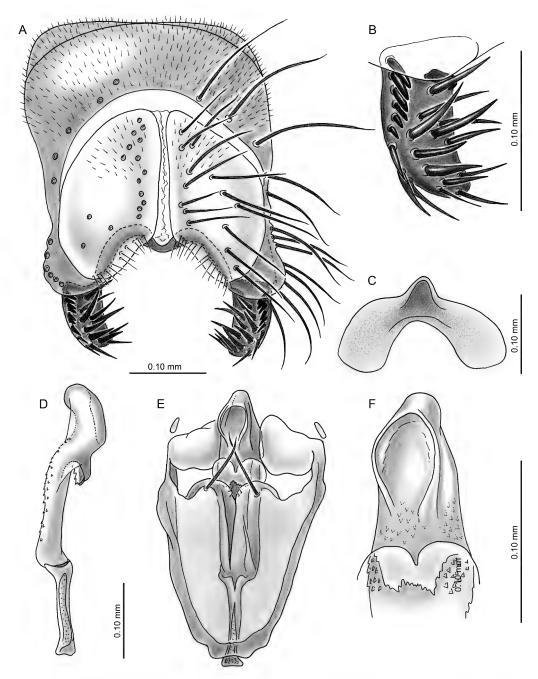


FIG. 23. *Hirtodrosophila florida*, n. sp., male terminalia (diss. no. 59). **A.** Epandrium and associated structures. **B.** Surstylus. **C.** Subepandrial sclerite, fully ventral view. **D.** Aedeagus and aedeagal apodeme, lateral. **E.** Hypandrium, aedeagus and aedeagal apodeme, ventral. **F.** Apex of aedeagus, ventral.

(posterior katepisternum), anterior katepisternum fine, ca.0.4× length of other, a minute seta between these. **Legs:** Forefemur with ventral row of 4 setae, lateral row 4 setae, none longer than thickness of femur; mid- and hind femora without large setae. Male foretarsus without fine, erect setulae on dorsal surface; midtibia with large ventroapical seta, hind tibia with short, fine preapical dorsal seta.

Thorax and wing measurements (N = 4): ThL 1.00 mm (0.96–1.04), DC-index 0.72, S-index 0.40 (0.38–0.41), 4-V index 1.86 (1.82–1.95), 5-X index 1.70 (1.57–1.85), C-index 1.85 (1.70–1.92), hb-index 1.74 (1.58–1.81), ThL/WL 0.51 (0.49, 0.53), WL/WW 2.20 (2.19–2.22).

Male Terminalia: Epandrium with dorsal portion elongate, microtrichia overall except for ventral lobes; ca. 15 setae in lateral row, longest ones dorsally, more numerous on ventral lobe: ventral lobe of epandrium short, broad, ends just below dorsal margin of surstylus. Subepandrial sclerite large, broadly arched with a small projecting lobe on posterior margin. Cercus large, broad, flattened, follows curvature of epandrial dorsum; slightly less sclerotized than epandrium; ventral margin of cercus oblique, slopes downward from middle laterad; microtrichia very sparse (on dorsal portion only), setae long, fine setulae in row on ventral margin. Surstylus pendulous, simple (no secondary lobes), dorsal portion covered by ventral epandrial lobe; dorsal row of 6 prensisetae pegs laterally, all other (ca. 15) prensisetae thick and setiform. Hypandrium well developed, relatively long; posterior lobes very light, membranous, without wrinkles, paraphyses with minute medial pair of setulae, large subapical seta. Aedeagus virtually straight in lateral view, with thicker apex; gonopore with slight rim, ledge or flap anterior to gonopore having fine, irregular serrations; fine, sparse scales on dorsal surface of aedeagal shaft. Aedeagal apodeme short, ca. 0.5× length of aedeagus, slender in lateral view.

Female Terminalia: Oviscapt with apex highly modified: preapical vertical row of 4 small pegs; ventral lobe with two large pegs projecting

terminally, horizontal row 8 minute pegs anterior to lobe along ventral margin. Oviprovector well developed; semicircular dorsally, with overlapping scales on dorsal margin appearing like saw teeth; scales abundant overall, overlapping. Spermatheca unique: hardly sclerotized; slender, roughly fusiform in shape; no introvert; with fine transverse wrinkles.

Type: Holotype, male. **USA: Florida**: Dade Co., near Homestead, 30/VI/92, D. Grimaldi. Not dissected, in AMNH.

Other Specimens Examined: **USA:** Florida: Dade Co., near Homestead, 30/VI/92, D. Grimaldi, on mushroom, 1 \(\) (dissected, no. 75), 2 \(\) (1 dissected, no. 59). Homestead, VII/31/59, W.B. Heed, 1 \(\) (AMNH).). All are paratypes (AMNH).

ETYMOLOGY: In reference to the state of the type locality, as a noun in apposition.

COMMENTS: I have not found this species in any material from the Caribbean, though most of the drosophilid collections I have examined are from Hispaniola, Puerto Rico, and the Virgin Islands, some from the Lesser Antilles, few from Cuba and Iamaica.

Hirtodrosophila grisea (Patterson and Wheeler)

Figures 6, 15E, 24, 25, 42, 43

Drosophila (Hirtodrosophila) grisea Patterson and Wheeler, 1942: 72.

DIAGNOSIS: A dark-bodied fly, largely brown with faint bluish pollinosity on head and thorax (pollinosity more apparent on female, as faint stripes on scutum); halteres white; legs light, yellowish; wing clear, unmarked, longer than body; abdominal coloration slightly dimorphic. Cheek relatively deep (CD/ED 0.24), wing long (ThL/WL 0.41), R₂₊₃ long (C-index 3.04). Surstylus with small dorsomedial lobe. Aedeagus slightly longer than aedeagal apodeme; extensively scaled in middle; apex rounded in dorsoventral views, slightly flattened.

DESCRIPTION: **Coloration**: Head: Frons mostly dark blackish brown, darkest on frontal

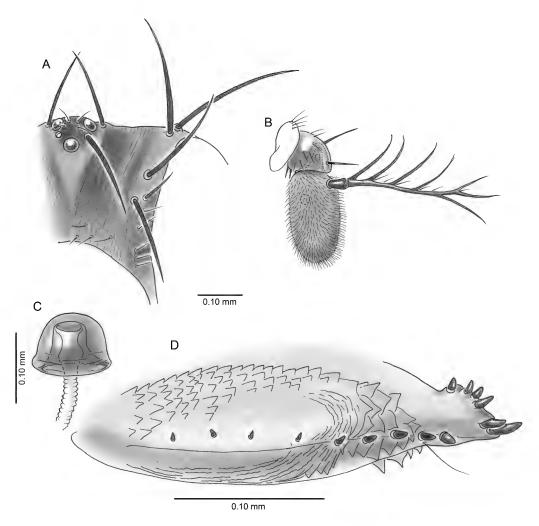


FIG. 24. *Hirtodrosophila grisea*, C, D female (diss. no. 80). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca. **D.** Oviscapt, lateral.

vittae, ocellar triangle, and at anterolateral margins; faint pollinosity overall, ocellar triangle and fronto-orbital plates slightly shiny. Antennal pedicel, basal flagellomere, carina light brown; rest of face lighter; lateral margins of ptilinal suture very light. Cheeks light, except for dark brown spot surrounding base of vibrissa and reaching to ventral margin of eye. Clypeus light brown, palps dark brown; most of proboscis cream colored, except for

labellum and labium, which are faint brown. Occiput dark brown; eye dark pinkish purple. Thorax: Mostly dark brown with faint bluish pollinosity overall, plus some light areas on postpronotal lobe, proepisternum, beneath wing base, on katepimeron; female with scutum having faint bluish-pollinose stripes (1 pair between dorsocentrals, another more lateral pair). Wing membrane clear, hyaline, no markings; veins light, fuscous brown. Halter

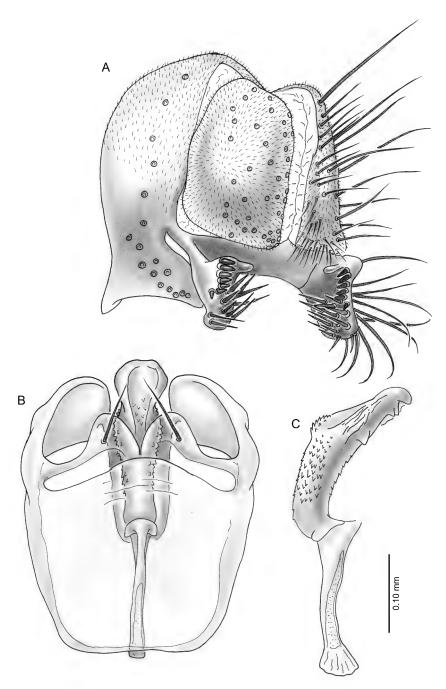


FIG. 25. *Hirtodrosophila grisea*, male terminalia. **A.** Epandrium and associated structures. **B.** Hypandrium, aedeagus, aedeagal apodeme, ventral. **C.** Aedeagus and aedeagal apodeme, lateral.

very light, whitish, small areas on stem slightly darker. Legs light, yellowish tan, mid- and hind coxae slightly darker. Abdomen with less pollinosity than on thorax, moderately shiny; in male mostly uniform light brown with pair of faint, dark yellowish spots on tergites 3 and 4; in female tergites 3–5 with yellowish areas forming short, transverse band, interrupted in middle by darker spot; oviscapt dark yellowish. Sternites lighter than tergites.

Head: Antenna: Scape and pedicel with setulae; pedicel with two larger setae; basal flagellomere with dense, light, short setulae; arista dark brown with relatively short branches, 5 dorsal ones and 1 ventral (opposite d5 or between it and d4), apical fork small. Eye suboval in lateral view, with dense, short interfacetal setulae. Carina narrow, fairly low, highest point near middle then receding toward oral margin. Vibrissa well developed, subvibrissal setae much smaller. Face and frons relatively broad. Frons: Fronto-orbital plates narrow, slightly shiny, end slightly anterior to proclinate; Fronto-orbital setae: proclinate relatively short; anterior reclinate slightly posterolateral to proclinate, about 0.5× size of posterior reclinate; posterior reclinate closer to proclinate than to verticals. Frontal vittae velvety, with scattered setulae on anterior portion, setulae are inclinate. Ocellar seta extended to slightly beyond proclinate; postocellar setae convergent; inner vertical seta slightly shorter than outer vertical. Palp relatively small, narrow, with single apical seta; labellum relatively small.

Head measurements (*N* = 2): CD/ED 0.24 (0.23, 0.25), ED/EW 1.22 (1.20, 1.24), FD/FW 0.76 (0.61, 0.92), FL/LFW 0.86 (0.85, 0.88), HW/HD 1.40 (1.37, 1.42), Ocellar S-index 1.05 (1.00, 1.09), OR1/OR3 0.74 (0.69, 0.79), OR2/OR1 0.60 (0.60, 0.61), VT-index 1.18 (1.16, 1.20).

Thorax: Acrostichal setae in 6-8 rows, ones immediately anterior to transverse suture slightly longer; anterior dorsocentral ca. $0.65 \times$ length of posterior dorsocentral; posterior dorsocentral close to anterior margin of scutellum (approximately $0.3 \times$ the seta length). Anterior scutellars

parallel, slightly longer than posterior ones; posterior scutellars crossing for about one-third their length. Two postpronotal setae; 2 setae at edge of notopleural suture (posterior one short), 1 long seta dorsal to these; 3 supra-alar setae (anterior one short, posterior one very long), 1 small postalar seta. Three katepisternal setae: anterior one ca. 0.5× size of posterior one, small middle one ca. 0.25× size of posterior seta.

Legs: Apical half of forefemur with row 3–4 long dorsolateral and 3–4 long ventrolateral setae, male foretarsus without long, fine erect setulae on dorsal surface. Middle femur without long setae; mid-tibia with long, stout ventroapical seta; hind femur without long setae, hind tibia with preapical dorsal seta.

Thorax and wing measurements (N=3): 4-V index 1.63 (1.59–1.70), 5-X index 1.59 (1.48–1.65), C-index 3.04 (2.93–3.23), DC-index 0.79 (0.66, 0.93), hb-index 1.93 (1.87–2.0), S-index 0.48, ThL 1.21 mm (1.15, 1.28), ThL/WL 0.41, WL/WW 2.28 (2.25–2.30).

Male Terminalia: Epandrium evenly arched, width approximately equal to height; anterodorsal phragma not developed; dorsal half with microtrichia, lateral portions with irregular row of ca. 20 setae; ventral lobe short, broad, ventral margin flat. Cercus well developed, not connected to epandrium; entirely microtrichose, tuft of fine, small setae on ventromedial corner; without ventral lobes. Surstylus with small dorsomedial lobe; row of 6 prensisetae dorsally, ventral portion of surstylus with ca. 10 stiff, stout setae; no microtrichia. Hypandrium large, anterior margin flat; posterolateral lobes well developed (1 pair), without microtrichia; paraphyses prominent, lobate, each with long fine seta. Aedeagus slightly curved in lateral view, slightly flattened dorsally; with dorsal, lateral, and some ventral scales in middle; apex rounded in dorsoventral view, ventrally with thick rim; slightly longer than aedeagal apodeme.

Female Terminalia: Oviscapt relatively narrow in lateral view, with about 15 pegs: 4 dorsal-preapical pegs, 2 large apical pegs, row of 9 pegs

along ventral margin, decreasing in size anteriad. Oviprovector well developed, scales well developed, larger toward apex. Spermatheca well sclerotized, slightly campanulate, introvert extended to ca. 0.85× length of capsule.

Types: A pin-mounted holotype does not exist in the AMNH (which would have been deposited along with the types of *H. longala* and *H. orbospiracula*, which are in the AMNH). I am designating two glass slide-mounts from the former UT slide collection as the holotype since these correspond to the sole locality and date described by Patterson and Wheeler (1942): **USA: Arizona**: Cochise Co., Rustler's Park, top of Chiricahua Mts., Aug. 17–18, 1941, lot 1242.8. Two slides: A, male genitalia (has two epandria; epandrium closest to the hypandrium + aedeagus is designated the type); B, two wings.

OTHER SPECIMENS EXAMINED: **USA:** Arizona: Pima Co., Mt. Lemmon, 7500 ft., D. Grimaldi, 18/IV/90, congregating in cave, $3 \, \mathring{\circ}$, $48 \, \mathring{\circ}$ ($1 \, \mathring{\circ}$, $1 \, \mathring{\circ}$ dissected: nos. 5, 80 respectively) (AMNH). Cochise Co., Chiricahua Mtns., Rustlers Park, VIII/2000, John Jaenike coll., $5 \, \mathring{\circ}$ (1 dissected, no. 7), $3 \, \mathring{\circ}$ (AMNH).

COMMENTS: Patterson and Wheeler (1942) described the internal reproductive organs of both sexes. The series that I collected on Mt. Lemmon in Arizona was part of an aggregation of thousands of specimens on the walls of a small cave, where they probably overwintered. There were very few males in the aggregation.

Hirtodrosophila jaenikei, new species

Figures 7, 15F, 26

Drosophila (Hirtodrosophila) nigrohalterata Duda, 1925: Wheeler, 1981, pg. 53 (misidentification).

DIAGNOSIS: As for the *H. nigrohalterata* complex: notum light brown; thin, dark brown stripe just below notopleural suture; pleura mostly light but with dark brown katepisternum, anepimeron, and katatergite; halter bulb dark brown, wing short, hyaline, no markings. Differs externally

from other nigrohalterata complex species: frontal vitta light, yellowish, ocellar triangle brown (vs. frons unicolorous), tergites 1-4 entirely brown (male only?), without pair of light spots on lateral margins. Anterior reclinate orbital seta anterolateral (vs. lateral or slightly posterior to) proclinate orbital seta; frons relatively long (frontal index 1.00), face deep (FD/FW 1.28); cheek shallow (CD/ED 0.12); anterior katepisternal seta relatively small (S-index 0.34); vein R₂₊₃ relatively short (C-index 1.59). Male genitalia differ from nigrohalterata and other species in complex as follows: cercus without small, setose medioventral lobe; ventral epandrial lobe with ca. 6 setae, lengths approximately same as lobe; surstylus with short row of 5 dorsal peg prensisetae (vs. 7-8); aedeagus apically pointed (vs. rounded), highly asymmetrical, with left margin having pointed lateral lobe (vs. rounded) and coarse serrations.

DESCRIPTION: Coloration: Head: Anterior portion of frons, frontal vittae cream colored, latter finely striate; ocellar triangle brown, matte (dark brown between ocelli), frontoorbital plates light brown, slightly shiny. Antennal pedicel light, with slightly infuscate mesal margin; basal flagellomere brown, with light setulae; arista with tiny basal articles light, branched portion dark. Face and cheeks whitish, with thin brown area near vibrissa. Clypeus light brown, palp dark brown, labellum light brown, rest of proboscis lighter. Thorax: Scutum light brown, anterior portion lighter, almost tan, with brown central area (approximately same color as ocellar triangle) between tangents through dorsocentrals, scutellum slightly lighter; notum slightly pollinose. Pleura largely light, cream colored, with several brown areas: a narrow stipe just under notopleural suture, most of katepisternum, all of anepimeron and katatergite. Wing entirely hyaline, no markings. Halter bulb dark brown; stem partially brown. Legs almost entirely light, cream colored, mid- and hind femora with slight infuscation at apex of femur and base of tibia. Abdomen (male only): tergites

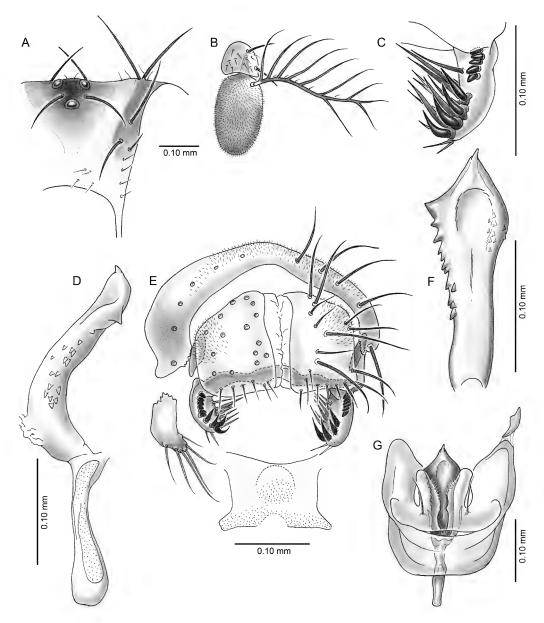


FIG. 26. Hirtodrosophila jaenikei, male holotype. A. Frons, portion. B. Antenna. C. Right surstylus. D. Aedeagus and aedeagal apodeme, lateral. E. Epandrium and associated structures (ventral lobe of epandrium shown detached, subepandrial sclerite shown in full ventral view). F. Aedeagus, ventral. G. Hypandrium, aedeagus, aedeagal apodeme, ventral.

1–4 entirely brown (male only?), without pair of light spots on lateral margins; sternites very light, cream colored; epandrium light.

Head: Antenna: Very close together, pedicels in contact medially; scape concealed by ptilinal suture; pedicel with setulae and two larger setae; basal flagellomere not quite reaching oral margin, with short setulae only, arista with 1 ventral, 7 long dorsal branches, terminal fork small. Eve egg shaped in lateral view (ventral portion smaller), interfacetal setulae dense. short. Face narrow, tall, slightly concave; carina very narrow, confined to upper half of face; one pair vibrissae, subvibrissal setulae very small. Frons: Fronto-orbital plate narrow, shiny; frontal vitta finely striate, narrow; ocellar triangle large, anterior corner extends nearly to ptilinal suture, lateral margin approximately midway between median ocellus and posterior reclinate seta. Fronto-orbital setae: proclinate seta slightly longer than posterior reclinate; anterior reclinate lateral and slightly anterior to proclinate, anterior reclinate ca. 0.6× length of posterior reclinate; posterior reclinate much closer to ipsilateral orbitals than to verticals; reclinates in line with ipsilateral inner vertical, proclinate slightly medial to this tangent. Ocellar seta not quite reaching to proclinate; postocellar setae relatively large, crossed for ca. 0.4× their length; directed posteriad. Vertical setae equal in length; inner verticals upright, strongly inclinate; outer verticals posteriad, slightly laterally.

Head measurements: CD/ED 0.12, ED/EW 1.37, FD/FW 1.28, FL/LFW 1.00, HW/HD 1.26, Ocellar S-index 1.23, OR1/OR3 1.13, OR2/OR1 0.41, VT-index 0.95.

Thorax: Setation: Acrostichal setae in approximately 6 (irregular) rows; anterior dorsocentral seta finer than and $0.6 \times$ length of posterior dorsocentral, posterior dorsocentral slightly closer to scutellar margin than to anterior dorsocentral. Anterior scutellar setae slightly convergent, ca. $0.75 \times$ length of posterior scutellars; posterior scutellars crossed for $0.3 \times$ their length. Postpronotal lobe with two

setae; three notopleural setae, anterior and dorsal ones longest, equal in size; two supraalar setae, anterior one short; two postalar setae, anterior one very long. Posterior katepisternal seta very long, >2× length of anterior katepisternal; a fine, short seta between them. **Legs:** Forefemur with ventral row of three longer setae on distal half, laterally with two such setae, setae not quite as long as femur width; mid- and hind femora without long setae. Male foretarsus without fine, erect setulae on dorsal surface. Midtibia with stout long ventroapical seta, hind tibia with short, fine erect seta.

Thorax and wing measurements: ThL 0.79 mm, DC-index 0.60, hb-index 1.72, 5-X index 2.72, S-index 0.34, ThL/WL 0.47, C-index 1.59, WL/WW 2.27, 4-V index 2.36.

Male Terminalia: Epandrium short, very broad; microtrichia on dorsal surface only; row 5-6 lateral setae; ventral lobe narrow, short (not reaching to ventral margin of surstylus), with ca. 6 setae having lengths less than length of lobe. Subepandrial sclerite relatively large, very faintly sclerotized. Cercus broad, relatively flat, with few microtrichia (on dorsolateral margin only), ca. 10 setae; ventral margin relatively flat, with row of 6-7 fine setulae. Surstylus pendulous, simple, with short dorolateral row 5 short peg prensisetae; ventrolateral row large, spinelike prensisetae, thinner setiform prensisetae medially. Hypandrium short, broad, distal lobes not wrinkled; paraphysis lobate, with pair of minute setulae midway along mesal margin, large seta at base of paraphysis (not at apex). Aedeagus slightly longer than aedeagal apodeme, slightly curved in lateral view; with ca. 12 scales on left margin, plus pointed preapical lobe, right margin simple, no scales; apex of aedeagus tapered to fine point. Female Terminalia: Unknown.

Type: Holotype, male, handwritten label: "Homestead, Fla. July 31, 1959." In AMNH. Genitalia dissected (no. 69) and one wing removed, stored in microvial on pin with specimen. The handwriting is Heed's, and the field notebook entry for that day has "fuscohalt- like"

1 [specimen], sweeping Royal Palm Hammock in Everglades."

OTHER SPECIMENS EXAMINED: None, known only from type.

ETYMOLOGY: Patronym, for John Jaenike (University of Rochester), esteemed colleague and former mentor, in recognition of his work on the genetics and ecology of wild *Drosophila*.

COMMENTS: Wheeler (1981) listed H. nigrohalterata as occurring in the southern U.S. to Costa Rica. Actually, the current concept of this species, based on Duda (1925), is comprised of a complex of at least five cryptic species. Based on my dissections, the Florida species is distinct from all Caribbean and Central American species, as diagnosed above. Among the series of specimens currently at hand there are two species in Puerto Rico, a species in Costa Rica, and a species that occurs in Costa Rica and El Salvador (probably true nigrohalterata). These will be described elsewhere. The type locality of nigrohalterata is Turrialba, Costa Rica; the type is a female, which unfortunately does not have the diagnostic characters that separate species in this complex. The record of H. nigrohalterata from the area of Austin, Texas (Patterson and Stone, 1952), and cited by Vilela and Bächli (2004), cannot be assessed in lieu of a voucher specimen.

> Hirtodrosophila longala (Patterson and Wheeler) Figures 8, 16A, 27, 28

Drosophila (Hirtodrosophila) longala Patterson and Wheeler, 1942: 71.

DIAGNOSIS: Similar in size and body proportions to *H. grisea*, but lighter (particularly the pleura), with faint brown stripes and bluish pollinosity on scutum; diffuse, light brown stripe on uppermost portion of pleura; female slightly darker. Anterior reclinate orbital seta minute; aristal branches relatively short, carina well developed but short. Male: Small lobe on ventromedial corner of cercus; prensisetae

divided on two lobes on surstylus, lower lobe somewhat triangular; aedeagus with pair of preapical-lateral spines; margin of oviscapt unmodified.

DESCRIPTION: Coloration: Top of head and thorax brown, with bluish pollinosity on scutum, pleura and abdomen lighter and with faint patterns. Head: Frons dark golden, frontal vitta finely striate and shiny; ocellar triangle dark brown; fronto-orbital plates and lateral margin of frons light. Antennal scape light; pedicel and basal flagellomere dark to medium brown; carina and upper portion of face light, lower portion of face near oral margin dark brown; cheek light, with brown spot just below eye; vibrissal angle dark brown. Female markings slightly darker than in male. Clypeus and palps dark brown; labium and outside surface of labellum light brownish; occiput dark brown; eye light, dull red. Thorax: Scutum mostly light brown, with dark brown and bluish-pollinose markings as follows: pair of faint dark brown stripes between middle 6 rows of acrostichals, a pair of very light brown faint stripes lateral to these but between tangent of dorsocentrals; scutum lateral to tangent of dorsocentrals light brown (hue is between the darkest and lightest of the stripes); light brown areas with light bluish pollinosity; scutellar disk mostly dark brown, anterolateral portions lighter. Pleura mostly light yellowish tan, with light brown, infuscate area on upper half, darkest near notopleural edge, including lower portion of postpronotal lobe (upper part of lobe light yellowish), forming diffuse, light brown stripe on uppermost portion of pleura. Wing hyaline, no markings; veins faint grayish brown. Legs entirely light, cream colored. Abdomen with most tergites having dark to light brown, complete transverse band on posterior half, anterior half is light; tergite 6 and epandrium in male entirely light.

Head: Antenna: Scape and pedicel with setulae; pedicel with two larger setae; basal flagellomere with just short, fine, light setulae (without long setulae); arista with 1 ventral and 4–5 dorsal branches, branches relatively short; ventral branch between apical dorsal

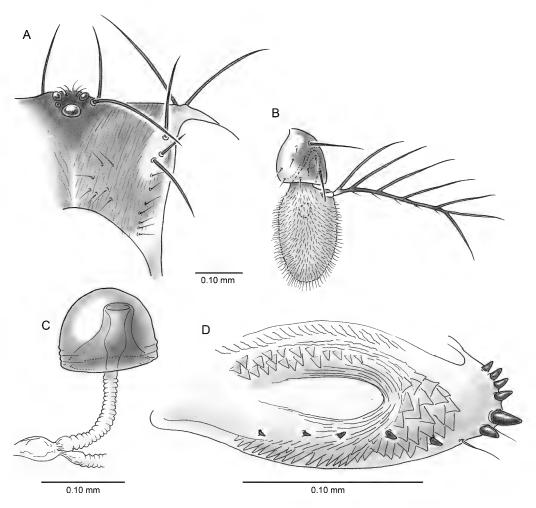


FIG. 27. *Hirtodrosophila longala*, C, D female (diss. no. 76). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca. **D.** Oviscapt, lateral.

branch and small apical fork. Eye egg shaped in lateral view (broader portion dorsally), taller than wide, with dense, light interfacetal setulae. Cheek of moderate depth. Face relatively broad; carina well developed but low, slightly flattened and broadened on lower portion. Vibrissa well developed, one pair, inclinate and nearly touching medially; subvibrissal setae very small. Frons: Relatively broad; frontal vittae relatively broad, anterior portion with ca. 12 small, scattered setulae, all incli-

nate; fronto-orbital plate narrow, ends slightly anterior to proclinate. Fronto-orbital setae: proclinate and posterior reclinate orbital setae approximately equal in size; anterior reclinate minute, barely differentiated from setulae on frons, located approximately midway and slightly lateral to other two, large orbitals; posterior reclinate closer to proclinate than to verticals. Ocellar triangle relatively large; ocellar setae long, widely divergent, tips extended to slightly past level of proclinates; postocellar

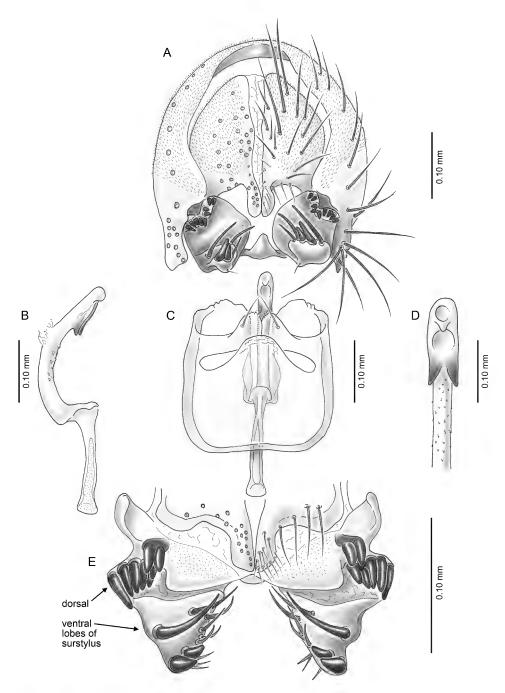


FIG. 28. *Hirtodrosophila longala*, male terminalia (diss. no. 12). **A.** Epandrium and associated structures. **B.** Aedeagus and aedeagal apodeme, lateral. **C.** Hypandrium, aedeagus, aedeagal apodeme, ventral. **D.** Distal half of aedeagus, ventral. **E.** Surstyli and ventral portion of cerci, in a more dorsal view than shown in A.

setae fairly long, tips crossing for approximately 0.2× the length. Inner vertical seta slightly longer than outer vertical, position of former significantly anterior, nearly in line with large orbital and outer vertical setae; outer vertical largely reclinate. Clypeus narrow; palps relatively small, with single large apical seta.

Head measurements (N=4): CD/ED 0.96 (0.18–0.22), ED/EW 1.28 (1.20–1.40), FD/FW 0.94, FL/LFW 0.85 (0.81–0.88), HW/HD 1.37 (1.32–1.46), Ocellar S-index 1.22 (1.10–1.38), OR1/OR3 0.94 (0.90–1.00), OR2/OR1 0.47 (0.33–0.50), VT-index 1.14 (1.06–1.18).

Thorax: Acrostichal setae in 8 rows, short transverse row of 3-4 larger ones immediately anterior to transverse suture. Anterior dorsocentral ca. 0.7× length of posterior dorsocentral; latter slightly sinuous; position slightly closer to scutellar margin than to anterior dorsocentral. Scutellar setae approximately equal in length, anterior pair parallel, posterior pair crossed for ca. 0.25× their length. Postpronotal lobe with two setae; notopleural edge with two setae (posterior one short), longer seta dorsal to these; 3 supra-alar setae, anterior one short, posterior one longest; postalar seta short, fine. Katepisternum with 2 large setae, middle (third seta) very small, not differentiated from setulae on katepisternum; anterior katepisternal seta approximately 0.5× length of posterior one. Legs: Forefemur with short row 2-3 long dorsolateral and 3-4 long ventrolateral setae, male without long, fine, erect setae on foretarus. Midfemur without macrosetae, midtibia with large ventroapical seta; hind femur without macrosetae; hind tibia with preapical dorsal seta.

Thorax and wing measurements: ThL 1.17 mm (1.14–1.25), DC-index 0.64 (0.62–0.68), S-index 0.45 (0.43–0.50), ThL/WL 0.42 (0.41–0.43), 4-V index 1.69 (1.60–1.79), 5-X index 1.47 (1.28–1.64), C-index 2.84 (2.79–2.93), hb-index 2.18 (2.0–2.46), WL/WW 2.26 (2.22–2.33).

Male Terminalia: Epandrium slightly higher than broad, with microtrichia on dorsal portion,

row of setae on dorsal half, denser setae (ca. 15) on ventral lobe; ventral lobe short. Cercus not connected to epandrium; overall with microtrichia, small tuft of fine setae on ventromedial corner. Surstylus relatively small, pendulous; with small dorsal lobe, lateral row of ca. 8 prensisetae, ca. 10 spinelike setae. Hypandrium well developed; posterolateral lobe small; paraphysis barely protuding, with microtrichia and single large seta. Aedeagus of moderate length, ca. 1.25× length of aedeagal apodeme; relatively straight, even in lateral view; with preapical pair of large spines laterally, sparse scales.

Female Terminalia: Oviscapt relatively simple and little modified, with marginal row ca. 11 pegs; apical peg largest one, 4 smaller dorso-preapical pegs, otherwise very little differentiation or gaps; oviprovector well developed, with coarse scales. Spermatheca well sclerotized, dome shaped, not annulated externally, introvert extended approximately $0.80 \times$ into length of capsule.

Types: Holotype, male. **USA:** New Mexico: label (typed): D. longala male, Greenwood, N.M. [New Mexico], G.B. Mainland, Col. 1941, Type. Patterson and Wheeler (1942) recorded the type as being from White Water Camp, Gila National Forest near Glenwood, October 1941. In AMNH. Another specimen kept with the type (a paratype: fig. 43) has a label also made with a typewriter; it simply says "D. longala female." This is actually a male of *H. grisea*, which I've labelled as such.

Other Specimens Examined: **USA: Arizona**: Cochise Co., Portal, Southwestern Research Station, VIII/2000, reared from fungus, J. Jaenike, coll. $\stackrel{\circ}{\circ}$ M, $3\stackrel{\circ}{\circ}$ (one of each sex dissected, nos. 12, 76 respectively).

COMMENTS: Patterson and Stone (1952) indicated this species occurs in the Mexican states (from north to south) of Chihuahua, Durango, Aguascalientes, and Michoacón, but I have found no specimens for these records and so cannot verify these identifications. Those authors also described the internal reproductive organs for both sexes.

Hirtodrosophila orbospiracula (Patterson and Wheeler)

Figures 9, 16B, 29

Drosophila (Hirtodrosophila) orbospiracula Patterson and Wheeler, 1942: 70.

DIAGNOSIS: Known only from male. Like *H. chagrinensis* tergites 1–5 each with completely transverse dark posterior bands; distinctive among all North American species for the light head and body (even the basal flagellomere and palp) and yellowish wing; acrostichals in front of anterior dorsocentral enlarged, carina relatively well developed. Male: Aedeagus largely devoid of scales, with large lateral pair of forward-pointing lateral spines.

DESCRIPTION: Coloration: (based on male only) Head: frons almost unicolorous, with faint differentiation among sclerites; frontal vitta finely striate, golden; ocellar triangle with lateral sides slightly lighter (area between ocelli slightly darker), shiny; fronto-orbital plate slightly lighter than vitta, shiny. Antenna: Scape light yellow, pedicel slightly darker, basal flagellomere dark yellow/tan, setulae very light, arista brown. Face light (very slight darkening at base of vibrissa), carina lighter; cheek, clypeus, palp, and proboscis light. Thorax: Scutum and scutellum evenly dark yellowish, pleura lighter; legs and halter very light, cream colored; wing faintly yellow. Abdomen: Tergites 1-5 each with completely transverse dark brown band on posterior half (tergite 1 with band lighter in middle), anterior half yellow, tergites 6, 7 all yellow. Sternites and epandrium light.

Head: Antenna: Scape with several fine setulae; pedicel with setulae and two larger setae; basal flagellomere short, apex not reaching oral margin, setulae very light, of moderate length (longest at apex of flagellomere); arista with 1 ventral, 7 dorsal branches, plus small terminal fork. Eye slightly egg shaped in lateral view, posterior margin slightly flattened; interfacetal setulae short, dense. Face of moderate height and depth, oral margin slightly concave; carina relatively well developed,

narrow (ca. 0.8× greatest width of basal flagellomere), edge slightly flattened, length approximately 0.75× the face depth. One pair vibrissae; subvibrissal setulae very small; cheek of moderate depth; palp with single large, subapical seta. Frons: Sclerites best distinguished in anterior view of head; fronto-orbital plates narrow, shiny; frontal vitta narrow, minutely striate; ocellar triangle seemingly long and narrow, anterior corner reaching to slightly past level of proclinates. Frontoorbital setae: proclinate slightly shorter than posterior reclinate; anterior reclinate small, ca. 0.3× length of posterior reclinate; posterior reclinate slightly closer to proclinate than to inner vertical; ipsilateral proclinate, posterior reclinate and inner vertical setae in line, anterior reclinate slightly lateral to this tangent. Ocellar seta not reaching to proclinate; postocellar setae ca. 0.65× length of ocellar, crossed at tips. Vertical setae long, equal length; inner verticals upright, inclinate; outer verticals lateroclinate, pointed slightly posteriad.

Head measurements: CD/ED 0.15, ED/EW 1.40, FD/FW 0.97, FL/LFW 1.02, HW/HD 1.31, Ocellar S-index 1.80, OR1/OR3 0.94, OR2/OR1 0.38, VT-index 1.12.

Thorax: Setation: Acrostichal setae in 8 rows, with short, graded row larger acrostichals immediately anterior to dorsocentrals (acrostichal closest to anterior dorsocentral nearly equals its length). Anterior dorsocentral 0.65× length of posterior dorsocentral; posterior dorsocentral about midway between anterior dorsocentral and scutellar margin. Anterior scutellar setae divergent, equal in length to posterior scutellars, latter crossed at apical third. Postpronotal lobe with 2 setae; 3 notopleural setae (two lost, relative lengths unknown); 2 supra-alar setae (posterior one very long) [postalar, katepisternal setae lost from specimen]. Legs: Fore femur with ventral row of 4 long setae, lateral row of 4 long setae; longest setae greater than width of femur; male fore tarsus without fine, erect setulae on dorsal surface. Mid and hind femora without long setae: mid tibia with large ventroapical seta; hind tibia with short, fine preapical-dorsal seta.

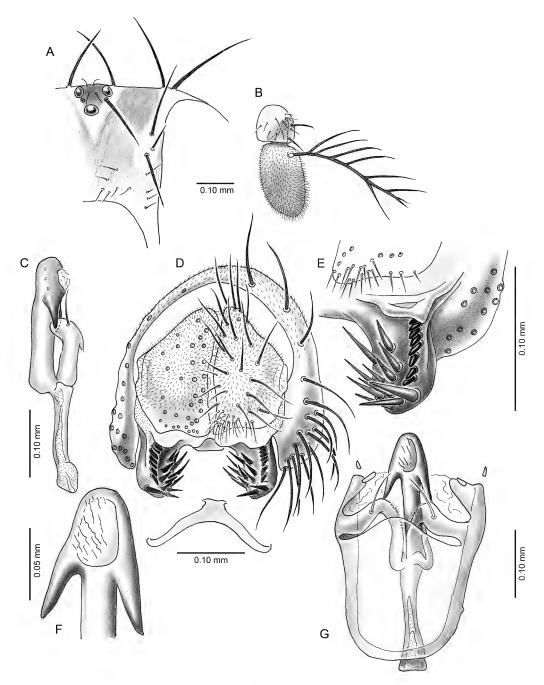


FIG. 29. *Hirtodrosophila orbospiracula*, male holotype. **A.** Frons, portion. **B.** Antenna. **C.** Aedeagus and aedeagal apodeme, lateral. **D.** Epandrium and associated structures (subepandrial sclerite shown detached, in full ventral view). **E.** Surstylus. **F.** Apex of aedeagus. **G.** Hypandrium, aedeagus, aedeagal apodeme.

Thorax and wing measurements: 4-V index 1.90, 5-X index 1.59, C-index 2.77, DC-index 0.65, hb-index 2.65, ThL 1.07, ThL/WL 0.47, WL/WW 2.28.

Male Terminalia: Epandrium arched, with microtrichia on dorsal half only; dorsolateral row of 5-6 setae, ventral lobe with group ca. 14 setae; lobe thick, short, not reaching to ventral margin of surstylus. Subepandrial lobe wide and short. Cercus not connected to epandrium: entirely microtrichose and setose; ventral margin with fine setulae on mesal corner. Surstylus pendulous, simple, with dorsolateral row 8 peg prensisetae, ca. 12 spiniform prensisetae more medially. Hypandrium well developed, relatively long, almost reaching to apex of aedeagal apodeme; posterolateral lobes turned inward, not wrinkled; paraphysis short, broadly and shallowly protruding, with microtrichia on mesal surface, large seta near middle. Aedeagus slightly longer than aedeagal apodeme, straight in lateral view; with lateral pair of large, forward-pointing, hooklike lobes; aedeagus with few, sparse scales toward apex. Female Terminalia: Unknown.

Types: Holotype male, on label: D. orbospiracula male, Chisos Mts. **Texas**, Mainland & Wagner Collectors, 1941, Type. In publication: "Upper Oak Creek, Chisos Mountains, Brewster County, Texas, August 13, 1941" (Patterson and Wheeler, 1942). Type in AMNH, the genitalia of which I have dissected.

OTHER SPECIMEN(s) EXAMINED: Patterson and Wheeler (1942) mentioned that a female was collected with the holotype male, but I have not found that specimen. The only other specimen is another male from the same locality as the type (1232.1 in the field notebooks), mounted on two glass slides: one slide with the legs, wings, and antennae, the other with genitalia.

COMMENTS: The abdominal color pattern is most similar to that of *H. chagrinensis*, but the opposite sexes of both species can be easily separated since *chagrinensis* has the basal flagellomere and palps dark brown (vs. yellowish), and a carina that is much smaller (in

fact, barely present). Patterson and Wheeler (1942) described the internal reproductive organs of the male and female, the puparium, and metaphase chromosomes of *H. orbospiracula*. In lieu of specimens I cannot confirm the record from Hidalgo, Mexico, reported by Patterson and Wheeler (1942) and cited by Vilela and Bächli (2004).

Hirtodrosophila ordinaria (Coquillett)

Figures 10, 11, 16C, 30, 31, 32

Drosophila ordinaria Coquillett, 1904: 190. Drosophila melanderi Sturtevant, 1916: 337. Synonymy by Lacy, 1981.

Drosophila magnafumosa Stalker and Spencer, 1939: 112. Synonymy by Lacy, 1981.

DIAGNOSIS: Coloration sexually dimorphic (males darker), highly variable (darker in individuals from cooler seasons and latitudes), usually with frontal vittae partly to entirely orange; dorsum of thorax yellowish, usually with diffuse, light to dark brown median stripe that is widened posteriad; pleura from light and yellowish with very faint infuscation to mostly dark brown; wing hyaline, legs, and halter light. Arista with relatively short branches, 1 ventral, 4 dorsal; basal flagellomere with setulae short; carina narrow. Male: Ventral portion of cercus curved inward, bearing stout, spinelike setae; surstylus with small dorsal lobe having short row of prensisetae pegs, larger ventral lobe with various prensisetae; hypandrium short and broad; aedeagus with pair of preapical lateral lobes. Female: Oviscapt margin entire (no emargination or differentiation of pegs)

DESCRIPTION: Coloration: Highly variable, from largely yellowish to dark brown, apparently based on temperature during development and sex (males being darker). Head: Frons varying from yellow and orange to brown and orange, always with faint bluish pollinosity on dorsal portion in frontal view; frontal vitta varying from entirely matte orange or orange-yellow, to

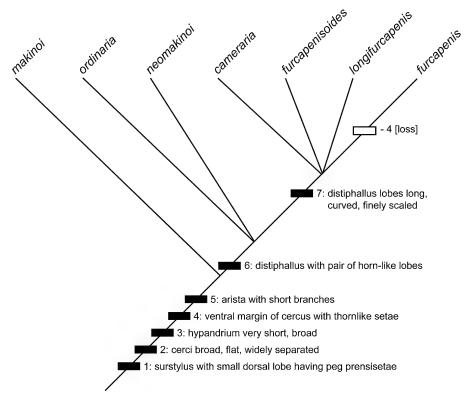


FIG. 30. Preliminary scheme of relationships in the Holarctic *Hirtodrosophila melanderi* species group. Species that are omitted are *H. shaitanensis* and *H. alpiniae* (see text).

just anterior portion orange with posterior portion brownish, always with ptilinal margin light, yellowish; ocellar triangle slightly shiny, yellowish to brownish outside of area of ocelli, always dark blackish brown within area of ocelli; frontoorbital plates yellowish to slightly infuscate, shiny. Antenna: Scape, pedicel light; basal flagellomere infuscate brown on anterior half. Face yellowish, light; cheeks slightly lighter, slightly darker at vibrissal angle. Proboscis: Clypeus same color as face or slightly darker; palps light yellowish, labellum slightly darker. Thorax almost entirely and evenly yellow, or like this but with diffuse, light to dark brown median stripe running down scutum and center of scutellum, stripe widened posteriad. Pleura varying from entirely light yellow with very faint brownish infuscation (beneath wing base and notopleural suture, sometimes dorsal portion of katepisternum), to mostly dark brown with some diffuse, lighter areas. Wing entirely hyaline, no markings; halter with knob cream colored, stem slightly darker. Legs entirely yellowish, coxae lighter. Abdomen: Tergites varying from mostly light yellow with faint, light brown infuscation on posterior and lateral margins (lateral margins are darkest), to largely dark brown; males with abdomen more extensively darkened; sternites very light yellow, cerci slightly infuscate.

Head: Antenna: Scape with row of setulae, pedicel setulose with two larger setae; basal flagellomere relatively short, apex reaching to lower level of carina, with short setulae only; arista with relatively short branches, 4 dorsal and 1

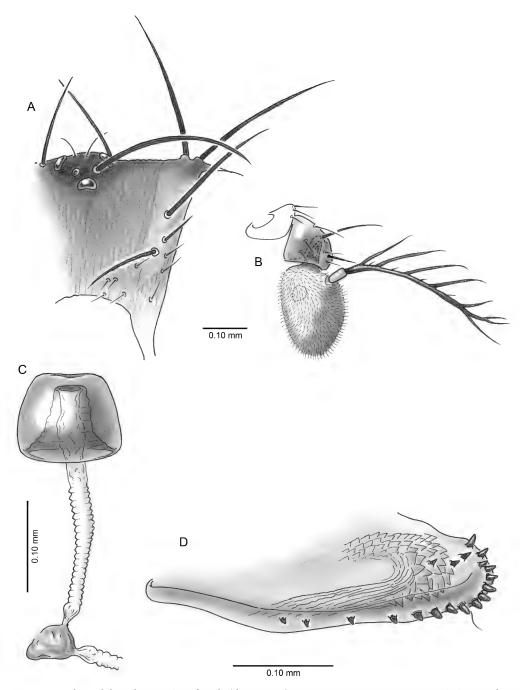


FIG. 31. *Hirtodrosophila ordinaria*, C, D female (diss. no. 83). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca (note slightly sclerotized junction of spermathecal ducts). **D.** Oviscapt, lateral.

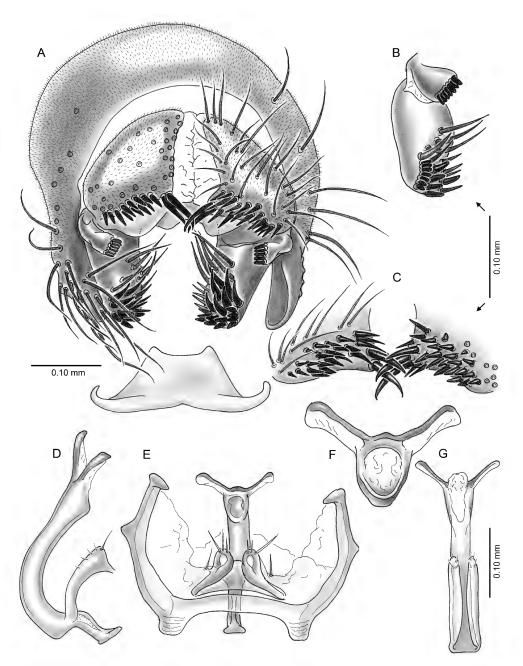


FIG. 32. Hirtodrosophila ordinaria, male terminalia (diss. no. 84). A. Epandrium and associated structures (subepandrial sclerite shown detached, in full ventral view). B. Surstylus. C. Spiny ventral surfaces of cerci, shown in full ventral view. D. Aedeagus and aedeagal apodeme, lateral. E. Hypandrium, aedeagus, aedeagal apodeme, ventral. F. Apex of aedeagus, ventral. G. Aedeagus, full ventral view.

ventral branch, plus short apical fork, ventral branch opposite last dorsal branch or between it and apical fork. Eye with short, dense micropubescence; slightly egg shaped in lateral view (dorsal portion larger). Face: Carina narrow, short (not reaching to oral margin), ventral portion deeper. Vibrissa well developed, points forward, one pair present, subvibrissal setae all much smaller. Frons: Fronto-orbital plates matte, very finely striate; orbital plates and ocellar triangle slightly shiny. Fronto-orbital setae: Proclinate slightly shorter than posterior reclinate; anterior reclinate quite small, ca. 0.3× size of other orbitals, slightly differentiated from scattered small setulae on anterior portion of frons; proclinate, posterior reclinate and inner vertical in line, anterior reclinate slightly lateral to this tangent. Ocellar triangle fairly large, anterior point reaching to level of proclinates. Ocellar setae close, within area bordered by ocelli, very long (tips extended past level of proclinate sockets); postocellar setae ca. 0.65× length of ocellars, slightly thicker, parallel. Inner vertical setae strongly inclinate; outer verticals strongly lateroclinate, both pairs about same size. Proboscis relatively short, virtually all withdrawn into oral cavity at rest, labellum small; palp with single, preapical seta.

Head measurements (N=4): CD/ED 0.19 (0.16–0.22), ED/EW 1.27 (1.22–1.33), FD/FW 1.06 (1.03–1.10), FL/LFW 0.91 (0.88–0.94), HW/HD 1.43 (1.42–1.44), Ocellar S-index 1.28 (1.21–1.33), OR1/OR3 0.78 (0.76–0.82), OR2/OR1 0.44 (0.41–0.47), VT-index 1.07 (1.06–1.10).

Thorax: Setation: Acrostichal setae in 6 rows, ones near transverse suture not enlarged; anterior dorsocentral ca. 0.65× size of posterior ones; posterior dorsocentral about midway between anterior dorsocentral and scutellar margin. Anterior scutellars slightly convergent; posterior scutellars crossed for about half their length, slightly longer than anterior scutellars. Postpronotal lobe with two setae; notopleural area with 3 setae, dorsal one largest; 2 supra-alars (posterior one much longer), 2 postalars (one long, one short). Anterior katepisternal ca. 0.7× length of poste-

rior katepisternal, small seta between these ca. 0.5× size of anterior katepisternal. **Legs:** Forefemur with ventral row of 8 long, fine setae (lengths ca. equal to femur width), lateral row of ca. 4 fine, shorter setae; mid- and hind femora with only short setae; male foretarsus without fine, erect setulae; midtibia with thick ventroapical seta, hind tibia with preapical dorsal seta.

Thorax and wing measurements: ThL 1.15 mm (1.09–1.21), DC-index 0.57 (0.52–0.66), S-index 0.58 (0.51–0.64), 4-V index 1.47 (1.41–1.52), 5-X index 1.46 (1.23–1.72), C-index 2.89 (2.71–3.01), hb-index 2.05 (1.67–2.40), ThL/WL 0.44 (0.40–0.51), WL/WW 2.23 (2.16–2.29).

Male Terminalia: Epandrium evenly rounded, with row of ca. 6 setae on lateral surface, none dorsally, 12-14 setae on ventral lobe; microtrichia present over most of epandrium, except ventral lobes; ventral lobe of epandrium slender, extended almost to ventral margin of surstylus. Subepandrial sclerite roughly trapezoidal, with pair of short anterolateral arms. Cercus with microtrichia and large setae, ventral surface curved strongly inward and bearing group of ca. 25 stout, sharp, sclerotized, spinelike setae, 2-3 most medial ones largest and interdigitate with such spines on opposite cercus. Surstylus bilobed, with small dorsolateral lobe bearing comb of 5 prensisetae pegs; main lobe of surstylus pendulous, with ca. 15–18 mostly spinelike prensisetae (some peg ones laterally), ventral ones shortest, dorsal ones long, setiform. Hypandrium very short and broad, roughly horseshoe shaped; paraphysis simple, moderately sclerotized, digitiform in full ventral view, with 2 minute and 1 large seta at apex. Aedeagus arched in lateral view, in dorsoventral view bearing pair of hornlike lobes at apex, which are partially sclerotized; aedeagus without hairs or scales. Aedeagal apodeme very short.

Female Terminalia: Oviscapt lightly sclerotized, with apical margin entire (no differentiation of pegs); with 19–20 oviscapt pegs, including short row of 3 small dorsal ones. Oviprovector well developed, apical scales coarse; spermatheca well sclerotized, dome shaped, exterior without

striations or other ornamentation, apex slightly flattened, introvert ca. 0.8× length of capsule; small sac where spermathecal ducts meet is slightly sclerotized.

Type: Holotype, USA: New Hampshire, White Mountains. In USNM.

OTHER SPECIMENS EXAMINED: USA: Alaska: Anchorage, July 1960, M.R. Wheeler, W.S. Stone, 3000.3, 1♂ (AMNH, dissected by MRW, genitalia on slide). Montana: 1.5 mi N Fish Creek Campground, Glacier National Park, VII/28-29/47, 1762.7, M.R. Wheeler, F.A. Cowan, 2 & (1 dissected, no. 85) (AMNH). New York: Broome Co., Chenango Valley State Park, 30 August, 1982, D.A. Grimaldi, 1♀ (AMNH). North Carolina: Highland, banana bait, VIII.62, D.D. Miller, 1♀, 1♂ (dissected, MF-1) (AMNH). **Tennessee**-North Carolina: Smoky Mountains National Park, 4000 ft., (holotype male of magnafumosa, in USNM); Clingman's Dome, Great Smoky Mountains National Park IX/11/41, 1275.9, G.B. Mainland, R. Wagner, 2♂ (1 dissected, MF-3, AMNH). Vermont: Orleans Co., nr. Bald Mtn., 1650 ft. 44.793912, -71.987953, D. Grimaldi, 19-21/VI/2016, sweep netted in forest near stream (Mad Brook), 13, 19 (both dissected, nos. 84, 83 respectively). Mad Brook Farm, E. Charleston, VII/15-25/82, D. Grimaldi, 1♀ (AMNH). Washington: 10 mi. N. Raymond, 2186.2, VI/31-VIII/1/51, M.R. Wheeler, W.B. Heed, 1♀ (AMNH); Pierce Co., Tacoma, (holotype♀ of *melanderi*) (USNM).

COMMENTS: Very widespread across entire North America, principally in the north, and at higher elevations where it extends southerly into Tennessee and North Carolina (e.g., Lacy, 1981). Highly variable coloration seems to correspond to temperature, with darker specimens occurring in more northern latitudes, higher altitudes, and in spring and fall, similar to the situation in *Drosophila putrida* (Sabath et al., 1973). The dramatic color variation probably resulted in *ordinaria* being described three times.

Wheeler (1954) was the first to recognize that *H. ordinaria* "is quite similar in appearance to both *melanderi* and *magnafumosa*." Lacy

(1981) examined the types of all three species and confirmed their common identity. He briefly redescribed H. ordinaria and figured the male genitalia for the first time, although he depicted the lower surstylus lobe as just setose instead of with prensisetae. He mentioned his examination of genitalia for specimens from Ithaca, New York, and the Smoky Mountains, Tennessee, that he collected as well as specimens collected by H.T. Spieth in Trinidad, California (on the state's northern coast). I have not seen specimens from California, but given the distinctive structure of the male genitalia the identification is probably correct. It's uncertain whether all the distribution records reported by Lacy (1981, i.e., Massachusetts, Minnesota, New Hampshire, Quebec, Washington) were based on specimens that he examined or they were just reports of earlier literature.

It is possible that *Hirtodrosophila shaitanensis* (Sidorenko, in Toda at al., 1996) is a junior synonym of H. ordinaria (shaitanensis is a substitute name for neomakinoi Sidorenko, 1995, which was preoccupied by Hirtodrosophila neomakinoi [Gupta and Singh, 1981]). I suspect this synonymy because Sidorenko's (1995) description of the external features, and his figures (Sidorenko, 1995: figs. 1-5) of the male and female terminalia are consistent with ordinaria (though lacking in detail), including aedeagal structure and proportions, the blunt apex of the oviscapt, and the deep spermathecal introvert. Lastly, H. ordinaria occurs north to Alaska, and H. shaitanensis occurs in Primorskii krai, Russian Far East (opposite Hokkaido, Japan) and Irkutskaya oblast (just north of Mongolia), so a Beringian distribution is very plausible. Specimens from eastern Russia need to be directly compared in detail with North American material.

Hirtodrosophila ordinaria belongs to the melanderi species group, all six other members of which are Palearctic (Wheeler, 1954; Lacy, 1981; Bächli et al., 2004). Hirtodrosophila cameraria (Haliday), redescribed in detail by Bächli et al. (2004), is widespread throughout Europe, occurring even in northern Africa and the Near East, its

most northern record from the vicinity of Stockholm, Sweden (Bächli et al., 2004), although it is not reported from eastern Russia or Siberia (Toda et al., 1996). Hirtodrosophila makinoi (Okada) occurs in Japan and the Russian Far East, and H. neomakinoi (Gupta and Singh) was collected in wet conifer forest at 7500 ft elevation in Darjeeling, West Bengal, India. Three species occur in China: H. furcapenis (Zhang and Liang), H. furcapenisoides (Zhang and Liang), and H. longifurcapenis (Zhang and Liang) (Zhang and Liang, 1995). When described from New Guinea, Hirtodrosophila alpiniae (Okada and Carson) was affiliated with the melanderi group (Okada and Carson, 1980), but this is not entirely clear. On the one hand, it has a short, broad, U-shaped hypandrium, a bilobed surstylus, and large spines on the cercus, and was reported as breeding in fungi. On the other hand, it was also breeding in the flowers of a wild ginger (Zingerberaceae), and described as having the arista with "5 lower, very short branches," the carina "high and long," and the authors figure the cercus with two large spines on the posterior surface (vs. multiple spines or denticles on the ventral surface). This species also needs to be reexamined.

A preliminary scheme of relationships for the *Hirtodrosophila melanderi* species group is presented in figure 32 (omitting *H. shaitanensis* and *H. alpiniae*). It is based on seven morphological features, five of which broadly define the species group. *Hirtodrosophila makinoi* appears to be the most basal species, lacking the pair of slender lateral lobes on the aedeagus so distinctive to the other species.

Life history and host records are largely known for just two species in the *melanderi* group: *H. ordinaria* and *H. cameraria*. Both appear to be rather polyphagous, breeding in an array of fleshy basidiomycetes, though they are rare compared to the common mycophagous species in the *Drosophila quinaria* and testacea species groups. In North America, Lacy (1981, 1982) reported having reared *Hirtodrosophila ordinaria* from 16 genera of basidiomycete fungi, comprising some 1520 specimens out of more

than 20,000 drosophilids reared in total. I have very rarely encountered *H. ordinaria* in my rearings of mycophagous drosophilids from the northeastern United States (e.g., Grimaldi and Jaenike, 1984). In Britain (Basden, 1954; Buxton, 1960), and Switzerland (Burla and Bächli, 1968), *H. cameraria* has been reported as quite rare in mushrooms, although Shorrocks and Charlesworth (1980, 1982) reported that in Britain it is moderately abundant in certain species, such as *Phallus impudicus* and *Lactarius quietus*.

Hirtodrosophila pictiventris (Duda) Figures 12, 16D, 33, 34

Drosophila pictiventris Duda, 1925: 211.

DIAGNOSIS: Coloration distinctive, elaborate, with light, cream-colored areas and dark brown markings; frons and scutum dark brown, the latter with faint, light brown, pollinose stripes; pleura with three thick, dark brown stripes alternating with thinner, cream-colored areas; legs light with light brown fuscous areas; wing with crossveins slightly clouded; abdomen mostly dark brown, with light median stripe, tergites 2-6 with light lateral spots and tergites 2-4 with additional light spots near lateral margins. Basal flagellomere with short setulae, arista with relatively long branches, 8 dorsal, 1-2 ventral; face relatively deep (FD/FW 1.21), cheek shallow (CD/ED 0.11), wing relatively short (ThL/WL 0.50). Oviscapt with distal pegs differentiated (apical one largest, vertical row of three dorsal ones, with gap between them). Male: Epandrium with pair of very large, thick setae laterally; cercus flattened; aedeagus relatively short (only slightly longer than aedeagal apodeme), finely scaled on ventral surface; surstylus with lateral row of five peg prensisetae, plus numerous spinelike ones medially.

DESCRIPTION: Coloration: Head: Frons mostly dark brown, anterior margin and thin median stripe ochre; fronto-orbital plates slightly lighter than frontal vittae; ocellar triangle and

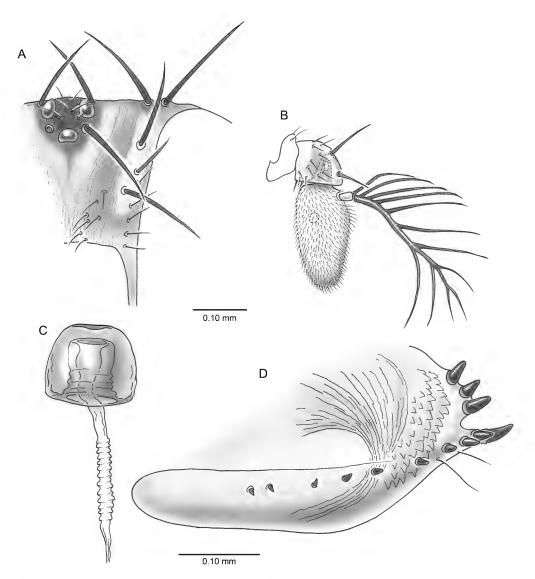


FIG. 33. *Hirtodrosophila pictiventris*, C, D female (diss. no. 8). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca. **D.** Oviscapt.

surrounding margin dark black-brown; light spot at base of outer vertical seta. Antenna with scape light, pedicel and basal flagellomere dark brown. Face light fuscous, lighter on oral margin; vibrissal angle and spot under cheek dark brown, cheek light; palp dark brown, clypeus slightly lighter; proboscis yellowish. Eye dark, dull red. Occiput dark brown. Thorax: Scutum dark brown, with faint light brown, pollinose stripes; light stripes coalesce on anterior portion of scutum, extending about 3/4 length of scutum; one stripe is median, two lateral to this (just inside dorsocentrals); lateral light stripe with short branch diverges toward supra-alar seta. Scutel-

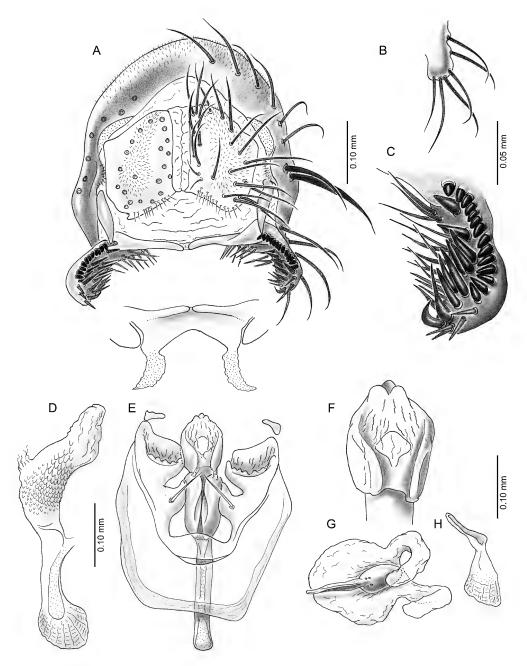


FIG. 34. *Hirtodrosophila pictiventris*, male terminalia. **A.** Epandrium and associated structures (subepandrial sclerite shown detached, in full ventral view). **B.** Ventral lobe of epandrium. **C.** Surstylus. **D.** Aedeagus and aedeagal apodeme, lateral. **E.** Hypandrium, aedeagus, aedeagal apodeme, ventral. **F.** Apex of aedeagus, ventral. **G.** Seminal vesicle with diverticula and ejaculatory apodeme in place. **H.** Ejaculatory apodeme, lateral view.

lum largely dark brown; postpronotal lobe light. Pleura with 3 dark brown, diffuse stripes, alternating with thinner, light, cream-colored stripes: 1 dark stripe from anterior edge to wing base, just under notopleural suture; another through middle of pleura, beginning just behind procoxa; third dark stripe covering all of katepisternum, meron, and metepisternum. Legs: All coxae light, cream colored; femora, tibiae, and tarsi light, fuscous brown, with slightly darker portions on femur (prebasally and preapically). Wing: Hyaline, only marking being slight infuscate cloud over crossveins and near wing base; veins brown. Halter with knob light, cream colored; stem light brown. Abdomen: Tergites mostly dark brown, with light median stripe through at least tergites 1-6, with row of light spots laterally on tergites 2-6; light spots lateral to this row on tergites 2-4, these coalesced on tergites 2 and 3. Little or no sexual dimorphism in coloration.

Head: Antenna: Scape with row of 5-6 fine setulae; pedicel setulose, with two larger setae; basal flagellomere of moderate length, tip at level of end of carina, setulae short; arista with 6-8 dorsal, 2 ventral branches plus small terminal fork, dorsal branches relatively long. Eye with dense, short interfacetal setulae; oval in lateral view, posterior margin slightly flattened. Face slightly raised, same width as lower part of frons; carina narrow, length ca. 0.65× depth of face. Vibrissa well differentiated from subvibrissal setulae, 1 pair; subvibrissal setae small. Frons: Fronto-orbital plates velvety, microscopically striate; fronto-orbital setae slender, slightly shiny. Anterior reclinate, posterior reclinate, inner vertical setae in line; proclinate seta slightly medial to this line, anterior (not lateral) to anterior reclinate; anterior reclinate seta midway between other orbitals, ca 0.4× length of proclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Ocellar setae extending to level of proclinates; postocellar setae ca. 0.7× length of ocellars, tips crossing at apical quarter. Inner vertical setae upright, slightly inclinate; outer vertical setae strongly lateroclinate, slightly longer than inner verticals. Clypeus narrow; palp relatively small, with single large, subapical seta; proboscis at rest almost fully retracted under head, labellum small and barely exposed. Cheek relatively shallow.

Head measurements (*N* = 4): CD/ED 0.11 (0.10–0.15), ED/EW 1.34 (1.27–1.40), FD/FW 1.21 (1.13–1.31), FL/LFW 0.94 (0.88–1.00), HW/HD 1.35 (1.21–1.43), Ocellar S-index 1.33 (1.23–1.50), OR1/OR3 1.04 (1.00–1.12), OR2/OR1 0.48 (0.38–0.66), VT-index 1.03 (1.00–1.15).

Thorax: Setation: Acrostichals in 6 rows, ones just anterior to transverse suture barely enlarged; anterior dorsocentral seta anterior to posterior dorsocentral by little more than length of anterior dorsocentral, slightly medial to posterior dorsocentral; anterior dorsocentral significantly finer than posterior dorsocentral. Anterior scutellars parallel, posterior scutellars crossed for about 0.5× their length. Postpronotal lobe with 2 short setae; 3 notopleural setae (1 dorsal, other 2 near notopleural suture); 1 short, 1 long supraalar setae; 1 short postalar seta. Anterior katepisternal significantly smaller than (ca. 0.5× the length) posterior katepisternal; two fine setulae between these. Legs: Forefemur with row of 4 long setae on ventrolateral surface; mid- and hind femora without such setae. Foretibia without larger setae; midtibia with ventroapical seta, hind tibia with preapical dorsal seta. Male foretarsus with a few very short, erect setulae on dorsal surface.

Thorax and wing measurements (*N* = 4): ThL 0.94 mm (0.86–1.08), DC-index 0.50 (0.39–0.63), S-index 0.48 (0.48–0.51), 4-V index 1.95 (1.85–2.00), 5-X index 1.82 (1.52–2.20), C-index 2.05 (1.87–2.36), hb-index 1.68 (1.53–1.84), ThL/WL 0.50 (0.49–0.51), WL/WW 2.19 (2.18–2.23).

Male Terminalia: Epandrium arched, rather broad, with lateral row of ca. 8 setae, ventral-most two setae very large and thick; ventral lobe of epandrium small, barely reaching to level of surstylus, with marginal row of ca. 6 fine setae. Small, slender sclerite isolated between ventral lobe of epandrium and surstylus (remnants of epandrium?). Cercus not connected to epandrium, slightly less sclerotized, with microtrichia; sparse fine setulae on flat-

tened ventral margin. Subepandrial sclerite large, with pair of faintly sclerotized and granular anterior arms. Surstylus pendulous, with dorsolateral row of heavily sclerotized 14-15 prensisetae pegs; middle row of large, sharp, sclerotized prensisetae; numerous finer ones medially. Hypandrium well developed; pair of large setae on paraphysis, two pairs smaller ones; posterolateral lobes concave, finely wrinkled. Aedeagus relatively short, about same length as aedeagal apodeme, apex slightly bulbous, membranous, without scales; shaft with fine overlapping scales ventrally. Ejaculatory apodeme relatively small, broadest portion a slender oval, at an oblique angle to apodeme. Female Terminalia: Oviscapt short, broad, oviscapt pegs as follows: vertical row of 3 dorsally, gap between this row and large apical peg; horizontal row ca. 9 pegs near ventral margin, significantly decreasing in size anteriad. Oviprovector well developed but scales relatively small and sparse. Spermatheca moderately sclerotized, dome shaped, externally smooth (not annulate or wrinkled), introvert ca. 0.8× length of capsule.

Type: Holotype, female, labelled "Higuito-San Mateo, Costa Rica, Schild 914, VII.16, *Drosophila busckii-ventris* n. sp. Det. Dr. O. Duda; *Drosophila pictiventris* n. sp. Type F, det. Duda." In HNHM, Budapest. The type specimen was examined by me in 2010, by Wheeler (1954, 1963), and by Bächli (1984), who mentioned (p. 34) that "According to DUDA, all species described in this 1925 paper should be labelled 'Suiza de Turrialba," which is another locality in Costa Rica where Schild extensively collected.

OTHER SPECIMENS EXAMINED: USA: Florida: Highlands Co., Lake Placid, Archbold Bio. Sta., M. Deyrup, emerged indoors 10 Oct. 1989 from Suillus sp. [Boletaceae], 66, 69 (16, 19 dissected, nos. 8, 9 respectively); emerged indoors 17 Oct 1989 from Clytocybe sp., 26, 29; emerged indoors 19 Oct. 1989 from Russula sp. [Russulaceae], 49, 16; emerged indoors 30 Oct 1989 from Suillus granulatus [Boletaceae], 29; emerged indoors 2 Nov 1989

from *Boletus* sp. $(6\,\,^{\circ}\,$, $1\,\,^{\circ}\,$), and from *Amanita* sp. [Amanitaceae], $1\,\,^{\circ}\,$; emerged indoors 1 Nov 1989 from *Russula abidula* [Russulaceae], $1\,^{\circ}\,$ (all AMNH). Archbold Biol. Sta. S.W. Frost, 12-29-64, 1 x (AMNH). Dade Co.: Homestead, VII/31/59, W.B. Heed, $1\,^{\circ}\,$ (dissected, no. 61) (AMNH); near Homestead, 30/VI/92, D. Grimaldi, $2\,^{\circ}\,$ (AMNH).

Based on my dissections of males, this is a very widespread species occurring from Florida, throughout the Caribbean, Central America, northern South America, and even the Galapagos. Male genitalia throughout the range are extremely uniform. Full neotropical distribution records will be provided elsewhere. Wheeler (1954) mentioned specimens he studied from San Andres Tuxtla, Vera Cruz (field notebook no. 2264.40) and Nochistlan, Oaxaca, Mexico; Soldedad, Cienfuegos, Cuba, and El Salvador. Wheeler's Vera Cruz records are associated with a series of 13 glass slides of at least 13 males. The specimen from Cienfuegos, Cuba (2083.2), is based on a slide mount of only the epandrium, so I cannot confirm the identity of that record, but it is likely correct given the widespread, distinctive nature of pictiventris.

COMMENTS: Wheeler (1954) provided a brief redescription based on new material, as well as a description of the egg (with four slender filaments), puparium, and internal reproductive organs. The species seems to thrive in scubby, seasonally to perennially dry habitats in the lowland neotropics, such as the Archbold Biological Station in Lake Placid, Florida, seasonal dry forest of Guanacaste Province, Costa Rica (it was an abundant species in Malaise trap samples from there), and even several of the Galápagos islands (Carson et al., 1983). The Galápagos are well known for not having any fresh water, and it has a very depauperate drosophilid fauna. Of the 16 species known from these islands, seven are introduced cosmopolitan species and perhaps only two are endemic; the rest are widespread neotropical species like H. pictiventris. Carson et al (1983) reported H. pictiventris on fungi in the mesic upland forests of Isla Santa Cruz and Isabella, but it is absent from the extremely dry, hot lowlands. Desiccation tolerance and (judging from Deyrup's host records from Florida) an ability to breed in diverse sorts of mushrooms probably account for the widespread distribution of this species.

Hirtodrosophila prognatha (Sturtevant)

Figures 13, 16E, 35, 36

Drosophila prognatha Sturtevant, 1916: 340.

DIAGNOSIS: Head, scutum, scutellum yellowish; pleura light, cream colored, with thin light brown band beneath notopleural margin (posterior segment often lacking), faint infuscation beneath wing base; anterior tergites light, infuscate brown, grading posteriad to yellow with narrow bands on posterior margins. Basal flagellomere with long setulae; arista with one ventral, five long dorsal branches; face slightly concave, relatively deep (FD/FW 1.17), with very small carina; frons relatively long (frontal index 1.07); anterior reclinate minute; anterior dorsocentral short (DCindex 0.50); wing short (ThL/WL 0.51), with faint infuscation near apex of Sc vein, vein R₂₊₃ short (C-index 1.62). Male: Surstylus small, with short vertical row ca. five prensisetae pegs; aedeagus short, stout, partially scaled, with distinctive notch at apex. Female: Oviscapt with ventroapical lobe, vertical row of four dorsal-preapical pegs.

DESCRIPTION: Coloration: Little or no sexual dimorphism in coloration. Head: Frons (including frontal vittae, fronto-orbital plates), face, antennae yellowish (branched portion of arista dark brown, tiny basal articles whitish); area between ocelli dark brown, outside ocelli is yellowish; cheek light yellow, with small light brown areas under eye and at vibrissal angle. Clypeus, palps, proboscis slightly lighter than rest of head, faintly dusky. Thorax: Scutum dark yellowish to light brown, graded from lighter at anterior end to darker posteriad; scutellum similar in coloration. Pleura mostly very light, cream colored, with thin, light brown stripe beneath notopleural suture, faint infuscation

beneath wing base usually present. Wing hyaline, no patterning. Legs light yellow; coxae lighter. Abdomen: Tergites 1 and 2 light brown (laterally yellow), tergites 3–4 with light brown transverse band on posterior margin, enlarged in middle on tergites 3 and 4, or most of dorsal surface of tergites 1–4 light fuscous brown, always laterally yellow; all of tergites 5, 6 yellow. Sternites, epandrium, cerci light yellow.

Head: Antenna: Scape largely hidden; pedicel setulose, with 2 setae; basal flagellomere long, tips extended slightly past oral margin, bearing dense, long setulae; arista with 1 ventral, 5 dorsal branches, ventral branch either between dorsal branches 4 and 5 or opposite the latter, branches relatively long, nearly 0.5× length of arista trunk. Eye in lateral view slightly egg shaped, ventral portion much smaller than dorsal portion; interfacetal setulae short, dense, light. Face slightly concave, relatively tall, with concave oral margin; carina very small and short, barely visible between antennae. One pair of vibrissae; subvibrissal setulae much smaller. Frons matte, unicolorous, with borders of fronto-orbital plates, frontal vittae and ocellar triangle barely differentiated, fronto-orbital plates finely striate. Fronto-orbital setae: proclinate approximately same length as posterior reclinate; anterior reclinate very small, ca. 0.25× size of other orbitals, slightly closer to and posterior to proclinate; fronto-orbitals in line with inner vertical. Ocellar seta relatively short, tips barely reaching to proclinate; postocellar setae crossed for ca. 0.3× their length. Inner vertical setae upright, slightly inclinate; outer vertical setae strongly lateroclinate. Proboscis short, retracted into oral cavity, with labellum exposed; labellum small; palp with one, preapical seta.

Head measurements (N=3): CD/ED 0.14 (0.12–0.16); ED/EW 1.23 (1.20–1.27), FD/FW 1.17 (1.11–1.24), FL/LFW 1.07 (1.03–1.10), HW/HD 1.25 (1.08–1.35), Ocellar S-index 1.34 (1.18–1.50), OR1/OR3 0.95 (0.80–1.06), OR2/OR1 0.36 (0.31–0.41), VT-index 1.10 (1.05, 1.15).

Thorax: Setation: Acrostichal setae in 6 rows; anterior dorsocentral short, ca. 0.6× length of

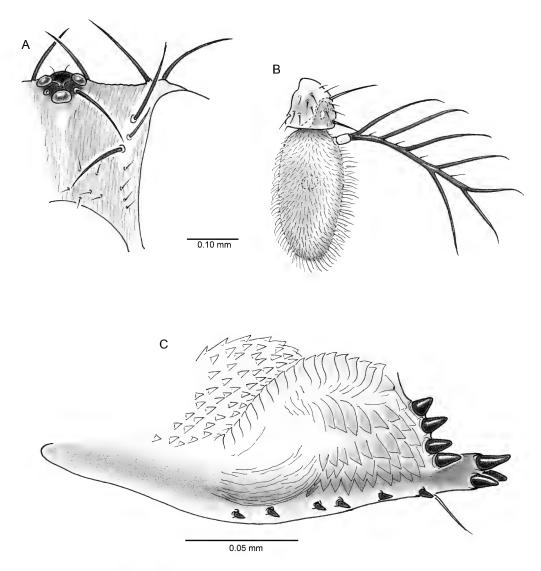


FIG. 35. Hirtodrosophila prognatha, C, D female (diss. no. 78). A. Frons, portion. B. Antenna. C. Oviscapt, lateral view.

posterior dorsocentral; posterior dorsocentral slightly lateral to longitudinal tangent through anterior dorsocentral. Anterior scutellars parallel, slightly shorter than posterior scutellars, lateral pair crossed for ca. $0.3\times$ their length. Two setae on postpronotal lobe; 3 notopleural setae, dorsal one small, fine, posterior one

short, thick; 2 supra-alar setae (posterior one long); 2 postalar setae. Anterior katepisternal seta small, ca. 0.5× length of posterior katepisternal. **Legs:** Fore femur with ventral row of 4 long setae, mid and hind femora without long setae; foretarsus of male without erect, fine setulae on dorsal surface; midtibia with large, ven-

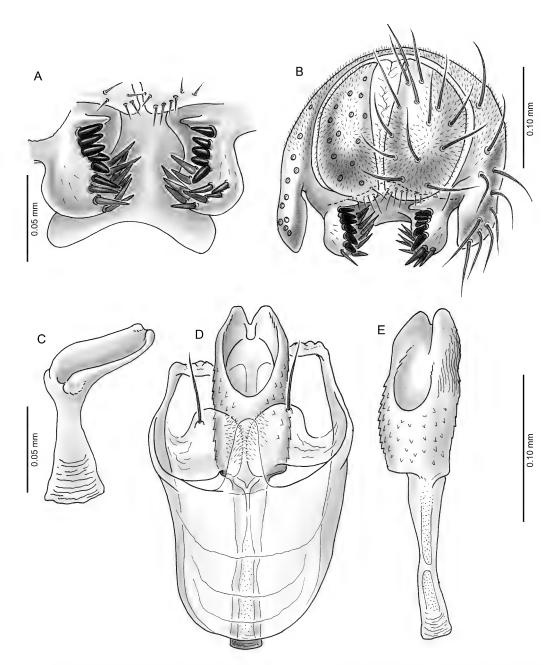


FIG. 36. *Hirtodrosophila prognatha*, male terminalia (diss. no. 13). **A.** Surstyli and subepandrial sclerite. **B.** Epandrium and associated structures. **C.** Ejaculatory apodeme. **D.** Hypandrium, aedeagus, aedeagal apodeme, ventral. **E.** Aedeagus, aedeagal apodeme, oblique dorsal.

troapical seta, hind tibia with small, fine, dorso-preapical seta.

Thorax and wing measurements: ThL 0.90 mm (0.76–1.01); DC-index 0.50 (0.43–0.57); S-index 0.47 (0.42–0.56); 4-V index 2.17 (2.07–2.28); 5-X index 2.10 (2.06–2.18); C-index 1.62 (1.41, 1.78); hb-index 1.75 (1.60–1.96); ThL/WL 0.51 (0.49, 0.52); WL/WW 2.16 (2.14, 2.18).

Male Terminalia: Epandrium evenly arched; with microtrichiae overall except for ventral lobes; ca. 5 setae laterally, plus ca. 5 setae on ventral lobe; ventral lobe of epandrium relatively short, not quite reaching to ventral level of surstylus. Cercus with microtrichia and setae; ventral margin with sparse, fine, short setulae. Surstylus simple, relatively small, with minute dorsal lobe just above prensisetae; short vertical row 5 prensisetae pegs dorsally, ventrally with ca. 10 stout setae. Hypandrium well developed, anterior margin rounded; posterior margin with medial lobe; paraphysis with microtrichia on mesal surface, 1 large apical seta; distal lobe slightly wrinkled. Aedeagus short, stout, approximately same length as aedeagal apodeme, largely membranous, with small, sparse scales basally on dorsal surface; apex with distinctive median notch.

Female Terminalia: Oviscapt with ventroapical lobe, bearing 3 pegs at apex; short vertical row of 4 preapical pegs; ventral margin with row of 6 small pegs. Oviprovector very well developed, scales large, well developed, shingled. Spermatheca dome shaped, with narrow collar of fine annulations; introvert about 0.5× length of capsule.

Type: Holotype, male (not dissected) **Puerto Rico**: Adjuntas, June 8–13, 1915, "TYPE" (red, printed label), "Am. Mus. Nat. Hist. Dept. Invert. Zool. No. 24149, Drosophila prognatha Sturtevant" (written label, in Sturtevant's hand). In AMNH.

OTHER SPECIMENS EXAMINED: **USA:** Florida: Alachua Co., Gainesville, Possum Creek Pres., 19/VII/2007, on fungus, S. Bybee, 19, 3 d (1 dissected, no. 13). **Puerto Rico**: Adjuntas, June

8–13, 1915, ["F3960b" on back of label], 6 $\stackrel{\frown}{\circ}$, 3 $\stackrel{\frown}{\circ}$ (dissected, no. 60), paratypes (all AMNH)

COMMENTS: I dissected several specimens from Sturtevant's paratype series from Puerto Rico, which perfectly match the Florida specimens. I also find that this species is remarkably similar to H. morgani (Mourão, Gallo, Bicudo), based on the original description and illustrations by Mourão et al. (1967), as well as the detailed redescription and illustrations of male terminalia by Vilela and Bächli (2004). Hirtodrosophila morgani is known from central to southern Brazil (Robe et al., 2014: states of Bahia, Paraná, Rondônia, and Santa Catarina) and may even occur in Argentina (Misiones) (Vilela and Bächli, 2004). In one study from Brazil it was found breeding primarily in Auricularia (Auriculariaceae) (Valer et al., 2016). Interestingly, ecological niche modeling based on the Brazilian records (Robe et al., 2014) predicts the occurrence of H. morgani throughout southern Brazil, Paraguay, northern Argentina, eastern Bolivia and Peru, western Ecuador, a small portion of central Venezuela, much of Central America and Hispaniola. I dissected prognatha-like male specimens from Belize, Panama, Colombia, French Guiana, and southern Venezuela, which had a uniform genital morphology (there were also several cryptic species). It appears that true H. prognatha is widespread at the very least throughout the Caribbean, Central America, and probably northern South America, but I need to examine Brazilian specimens to better assess their identity.

Hirtodrosophila thoracis (Williston)

Figures 14, 16F, 37, 38

Drosophila thoracis Williston, 1896: 411.

DIAGNOSIS: Relatively small fly with contrasting color: top of head and thorax dark brown; most of pleura and all of legs light cream color, thin dark brown band just below notopleural suture; abdomen mostly black-brown, with pat-

tern as described below. Basal flagellomere with long setulae; arista with 1–2 ventral, 4 long dorsal branches; anterior dorsocentral seta small, only ca. $0.4\times$ length of posterior dorsocentral. Face relatively deep (FD/FW 1.25), cheek shallow (CD/ED 0.10). Wing mostly clear with small, faint infuscate area below apex of Sc vein; vein R_{2+3} short (C-index 1.27). Anterior dorsocentral seta short (DC-index 0.46). Male: Cercus with fingerlike ventromedial lobe; surstylus broad, rounded; aedeagus virtually straight, apex almost round in ventral view, constriction between bulbous apex and neck. Female: Oviscapt margin entire, no differentiation of pegs at apex.

DESCRIPTION: Coloration: Little to no sexual dimorphism. Head: Frons with anterior portion light fuscous; posterior portion dark blackish brown. Frontal vittae matte, finely striate; ocellar triangle and fronto-orbital plates slightly darker, shiny; area bounded by ocelli dark, blackish brown. Face and carina light, oral margin, vibrissal angle and anterior portion of cheek fuscous brown; posterior portion of cheek light, cream colored. Antenna with scape light, pedicel and basal flagellomere light brown; arista dark with minute basal articles cream colored. Eye dark red. Clypeus light brown (same as oral margin), palp and rest of proboscis light (creamy). Thorax: Scutum and scutellum dark brown, scutum with faint, diffuse pair light paramedian stripes on anterior third. Pleura: Thin, dark brown stripe just below notopleural suture, extending from anterior edge of thorax to wing base; rest of pleura creamy white. Wing mostly hyaline, with small, faint infuscate area below apex of Sc vein; halter stem slightly infuscate, knob lighter. Legs entirely cream colored. Abdomen: Mostly blackish to black-brown, shiny; with light median stripe on tergites 1-3; tergite 4 with light transverse band on anterior half, small, light median triangle on posterior margin; tergites 5, 6 entirely or virtually all dark.

Head: Antenna: Scape bare; pedicel with setulae, 2 slightly larger setae; basal flagellomere of moderate length (apex not reaching to level of oral margin), with long, light setulae (especially

on anterior edge and apical half); arista with 1 ventral, 4 long dorsal branches, plus terminal fork, ventral branch between apical fork and d-4. Eye unevenly egg shaped in lateral view, posteroventral margin flattened; interfacetal setulae short, dense. Face: Width and depth moderate, slightly concave; carina small, narrow, on upper 2/3 of face. Vibrissae: 1 pair, subvibrissal setulae much smaller. Cheek shallow. Frons: Relatively flat; fronto-orbital plates shiny, narrow; frontal vittae finely striate, little differentiation between its edges and those of ocellar triangle. Frontoorbital setae: proclinate slightly longer than posterior reclinate; anterior reclinate tiny (ca. 0.3× size of proclinate), midway between ipsilateral orbitals; posterior reclinate much closer to proclinate than to verticals; reclinates and inner vertical in a line, proclinate slightly medial to this tangent. Ocellar seta extending to level of proclinate; postocellar setae ca. 0.5× length of ocellars, tips crossed. Inner vertical setae short, inclinate; outer vertical setae moderately lateroclinate. Proboscis short, at rest entirely withdrawn into oral cavity; labellum broad when opened.

Head measurements (*N* = 4): CD/ED 0.10 (0.08–0.14), ED/EW 1.24 (1.22–1.27), FD/FW 1.25 (1.15–1.33), FL/LFW 0.97 (0.93–1.07), HW/HD 1.48 (1.41–1.62), Ocellar S-index 1.28 (1.25–1.30), OR1/OR3 1.24 (1.12–1.33), OR2/OR1 0.42 (0.37–0.50), VT-index 0.92 (0.76–1.05).

Thorax: Setation: Acrostichal setae in 6 rows: anterior dorsocentral seta small, fine, ca. 0.4× length of posterior dorsocentral, latter closer to anterior dorsocentral than to scutellar margin. Anterior scutellar setae small (ca. 0.5× length posterior scutellars), parallel; posterior scutellars parallel to slightly convergent. Postpronotal lobe with 2 setae; 3 notopleurals, all equal in size; 2 supra-alar setae (posterior one longest); 2 postalar setae (anterior one very long). Katepisternum with 2 setae, anterior one short, ca. 0.4× length of posterior katepisternal. Legs: Forefemur with ventral row 4 erect, short setae, 1 lateral seta (lengths shorter than width of femur), mid- and hind femora without larger setae; male foretarsus with ca. 10 very fine,

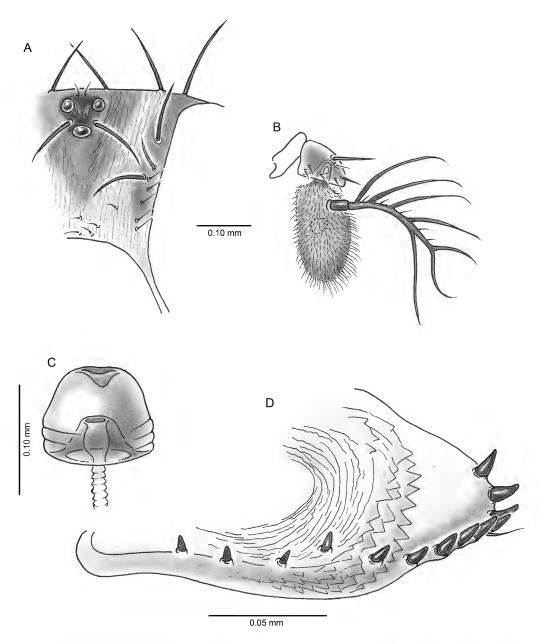


FIG. 37. *Hirtodrosophila thoracis*, C, D female (diss. no. 77). **A.** Frons, portion. **B.** Antenna. **C.** Spermatheca. **D.** Oviscapt, lateral.

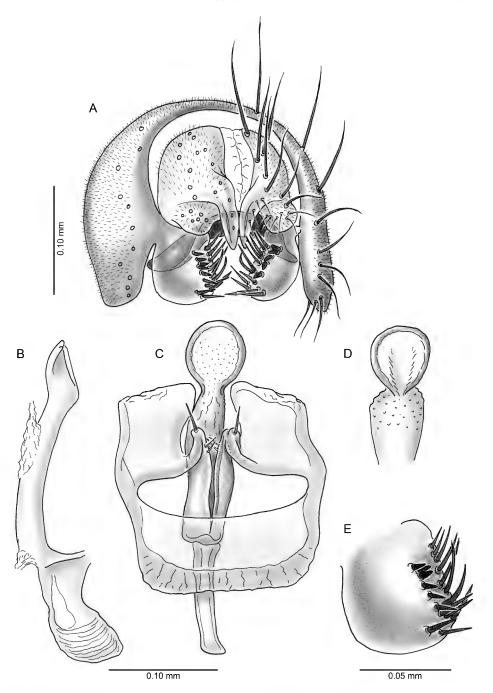


FIG. 38. Hirtodrosophila thoracis, male terminalia (diss. no. 14: Gainesville FL). A. Epandrium and associated structures. B. Aedeagus and aedeagal apodeme, lateral view. C. Hypandrium, aedeagus, aedeagal apodeme, ventral view. D. Apex of aedeagus, specimen from Rio Piedras, Puerto Rico (diss. no. 42). E. Surstylus.

short, erect setulae on dorsal surface. Midtibia with stout ventroapical seta; hind tibia with fine preapical dorsal seta.

Thorax and wing measurements (*N* = 4): ThL 0.79 mm (0.71–0.91), DC-index 0.46 (0.39–0.56), S-index 0.39 (0.36–0.45), 4-V index 2.41 (2.23–2.57), 5-X index 2.69 (2.53–2.72), C-index 1.27 (1.17–1.44), hb-index 1.64 (1.54–1.85), ThL/WL 0.46 (0.44–0.49), WL/WW 2.27 (2.22–2.35).

Abdomen: Relatively short, broad, somewhat dorsoventrally flattened. Male Terminalia: Epandrium broadly arched, with microtrichia overall (including ventral lobe), row of 8-10 setae on lateral surface, none dorsally; ventral lobe of epandrium relatively short, extending slightly past lower level of surstylus. Cercus not connected to epandrium, with fingerlike ventromedial lobe; broad, short ventrolateral lobe (both lobes with very fine setulae). Surstylus broad, rounded in full lateral view, with row 5-8 peg prensisetae lateral to some 10-12 setiform prensisetae on mesal and ventral margins; no microtrichia. Hypandrium moderately short and broad, anterior margin flat; paraphysis small, with pair of minute setulae mesally, stout seta at apex. In lateral view aedeagus slightly curved, aedeagal apodeme broad and keel shaped; aedeagus ca. 2× length of aedeagal apodeme; in ventral view tip of aedeagus subcircular to nearly circular, constriction between this portion and neck; dorsal surface of neck and bulbous apex sparsely, finely pimplate. Aedeagal apodeme extended well beyond anterior margin of hypandrium. Female Terminalia: Oviscapt with apical margin entire, no differentiation of pegs; marginal row of ca. 13 pegs, decreased in size anteriad; oviprovector well developed, scales coarse on posterior surface. Spermatheca dome shaped, with small terminal umbilicus; introvert short, ca. 0.45× length of capsule; exterior of capsule with 3 faint ribs at base.

Types: Two cotypes, from which a lectotype was designated here. "Windward Is[lands], St. Vincent, BWI [British West Indies], H.H. Smith/ W. Indies/ Drosophila thoracis" (hand-

written). In the Natural History Museum, London (not dissected).

Other Specimens Examined: **USA:** Arkansas: Logan Co., Magazine Mtn., 2750 ft., D. Grimaldi, VII/16/92, collected at 2200 ft. from oak sap flux, $1\mathbb{?}$ (AMNH). **Florida**: Orlando, June 26, 1953, M.R. Wheeler, on fungus, $4\mathbb{?}$, $6\mathbb{?}$ (1 of each dissected, nos. 30, 31 respectively) (AMNH). 14 mi. E. Orlando, cypress swamp area, [field notebook no.] 2314.8, VI/26–27/53, W. B. Heed, M.R. Wheeler, $3\male$, $1\male$ (AMNH). Alachua Co., Gainesville, Possum Creek Pres. 19/VII/2007, on fungus, S. Bybee, $1\male$, $2\male$ (1 dissected, no.14). **Louisiana**: Chicot S. Pk. [State Park] nr. Ville Platte, Sept. 1954, M. Wheeler, $4\male$ (1 dissected, no. 29), $2\male$ (AMNH).

COMMENTS: According to Wheeler (1981) this species occurs in the West Indies to the southeastern United States. Actually, it has an even wider distribution, perhaps the widest distribution of all New World Hirtodrosophila save H. pictiventris. Based on my dissection of dozens of male specimens throughout the range (including from St. Vincent, the type locality), the male genitalia are remarkably uniform throughout the range. Hirtodrosophila thoracis occurs in the north from Louisiana and Florida, throughout Central America and the Caribbean, south to central Brazil and Ecuador, Neotropical distribution records will be provided in detail elsewhere, along with the description of several new Neotropical species superficially similar to thoracis.

KEY TO HIRTODROSOPHILA SPECIES OF AMERICA NORTH OF MEXICO

2. Largely dark brownish-black species with solid, thin longitudinal stripe under notop-leural suture (fig. 14)
 thoracis (Williston) Largely light to dark yellowish or light brown; with short, diffuse marking under notopleu-
ral edge and wing base, or none3 3. With short, diffuse marking under notopleural
edge and wing base (fig. 13)prognatha (Sturtevant) - Without such markings4
4. Scutum light brown, with faint, incomplete pair of paramedian stripes; abdomen uninformly light brown (fig. 5)florida, n. sp.
- Scutum dark yellowish, without paramedian stripes (figs. 9C, D); posterior margin of
most abdominal tergites with dark transverse band (fig. 9E)
5. Dark transverse bands on posterior margins of tergites interrupted in middle (figs. 10D, 11D)ordinaria (Coquillett)
- Such bands not interrupted in middle, bands either of uniform thickness or widened in middle
6. Pleura with katepisternum, anepimeron and katatergite brown with discrete edges, rest of pleura light, cream colored (fig. 7B)
- Pleura with infuscation, from either faint and restricted to extensive, dark
7. Pleura with faint infuscation (fig. 4B), abdominal coloration sexually dimorphic (male is all dark; female tergites with dark posterior band that is expanded in middle; figs. 4C,
D), arista with two ventral branches (fig. 20B)duncani (Sturtevant)
 Pleura with extensive infuscation, male tergites very similar to those of female; arista with one ventral branch8
8. Posterior half of tergites 3, 4, 5 with dark brown transverse band of even width (anterior half is yellow) (fig. 3C), carina barely
developed (fig. 3B)

- Dark bands on tergites 3, 4, 5 thickened in middle9 9. Scutum light brownish, slightly shiny (fig. 8C), barely with grayish-brown pollinositylongala (Patterson and Wheeler) - Scutum dark brownish with distinct pattern of grayish pollinosity (figs. 2B, 12B)10 10. Dark tergal bands interrupted near lateral margins (figs. 12D, E), posterior crossvein (dm-cu) with faint infuscation (fig. 16)pictiventris (Duda) - Dark tergal bands not interrupted near lateral margins, dm-cu without infuscation11 11. Apex of cell Sc cell with small dark lappet (fig. 15A); carina barely developed (fig. 2A)alabamensis (Sturtevant) - Apex of Sc cell without small dark lappet; carina well developed12 12. Wing clear; Sc break without black spot; legs yellowishgrisea (Patterson and Wheeler) - Wing dusky; Sc break with black spot; legs grayish browncinerea1 (Patterson and Wheeler)

ACKNOWLEDGMENTS

I am grateful to Mark Deyrup and Seth Bybee, who provided specimens that they collected in Florida, and John Jaenike, who provided specimens from Arizona. The late William B. Heed showed me in 1995 the location of a cave in Arizona with diapausing H. grisea. Torsten Dikow (USNM) provided a loan of the type of H. chagrinensis, and Jason Dombroski (Cornell University) and Lynn Kimsey (University of California, Davis) checked their institutional collections for specimens of H. ordinaria collected by R. Lacy and H.T. Spieth, respectively; Erica McAlister (NHML) provided information on Williston's types in London. Steve Thurston (AMNH) assembled and labeled the plates from my photos and drawings. I am grateful for the

¹Key characters based on original description by Patterson and Wheeler (1942).

careful reviews by Gerhard Bächli and an anonymous reviewer.

REFERENCES

- Bächli, G. 1974. Revision der von Duda beschriebenen südostasiatischen Arten des *Drosophila*-Subgenus *Hirtodrosophila* (Diptera: Drosophilidae). Mitteilungen aus dem Zoologischen Museum in Berlin 49 (2): 267–315.
- Bächli, G. 1984. Catalog of the types of Drosophilidae in the Hungarian Natural History Museum, Budapest (Diptera). Folia entomologica Hungarica 45 (2): 27–41.
- Bächli, G., C.R. Vilela, A. Escher, and A. Saura. 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 39: 1–362. Leiden: Brill.
- Basden, E.B. 1954. The distribution and biology of Drosophilidae (Diptera) in Scotland, including a new species of *Drosophila*. Transactions of the Royal Society of Edinburgh 62: 603–655.
- Burla, H., and G. Bächli. 1968. Beiträg zur Kenntnis der schweizerischen Dipteren, insbesondere *Drosophila*-Arten, die sich in Fruchtkörpen von Hutpilzen entwickeln. Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich. 113: 311–336.
- Buxton, P.A. 1960. British Diptera associated with fungi III. Flies of all families reared from about 150 species of fungi. Entomologists' Monthly Magazine 96: 61–94.
- Carson, H.L., F.C. Val, and M.R. Wheeler. 1983. Drosophilidae of the Galapagos Islands, with descriptions of two new species. International Journal of Entomology 25 (4): 239–248.
- Coquillett, D.W. 1904. New North American Diptera. Proceedings of the Entomological Society of Washington 6: 166–192.
- Dorsey, C.K., and H.L. Carson. 1956. Selective responses of wild Drosophilidae to natural and artifical attrahents [sic]. Annals of the Entomological Society of America 49 (2): 177–181.
- Duda, O. 1923. Die orientalisches und australischen Drosophiliden-Arten (Dipteren) des Ungarischen National-Museums zu Budapest. Annales Historico-Naturales Musei Nationalis Hungarici 20: 24–59.
- Duda, O. 1925. Die costaricanischen Drosophiliden des Ungarischen National-Museums zu Budapest. Annales Historico-Naturales Musei Nationalis Hungarici 22: 149–229.

- Grimaldi, D.A. 1987. Phylogenetics and taxonomy of Zygothrica (Diptera: Drosophilidae). Bulletin of the American Museum of Natural History 186 (2): 103– 268.
- Grimaldi, D.A. 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). Bulletin of the American Museum of Natural History 197: 1–139.
- Grimaldi, D., and J. Jaenike, 1984. Competition in natural populations of mycophagous *Drosophila*. Ecology 65 (4): 1113–1120.
- Kohler, R.E. 1994. Lords of the fly, *Drosophila* genetics and the experimental life. Chicago: University of Chicago Press.
- Lacy, R.C. 1981. Taxonomic and distributional notes on some fungus-feeding North American *Drosophila* (Diptera, Drosophilidae). Entomological News 92 (2): 59–63.
- Lacy, R.C. 1982. Niche breadth and abundance as determinants of genetic variation in populations of mycophagous drosophilid flies (Diptera: Drosophilidae). Evolution 36 (6): 1265–1275.
- Mourão, C.A., A.J. Gallo, and H.E.M.C. Bicudo. 1967. Drosophila morgani, nova espécie brasileira (Drosophilidae, Diptera). Papéis Avulsos de Zoologia 20 (15): 159–164.
- Okada, T. 1956. Systematic study of Drosophilidae and allied families of Japan. Tokyo: Gihodo, 183 pp.
- Okada, T., and H.L. Carson. 1980. Drosophilidae associated with flowers in Papua New Guinea II. *Alocasia* (Araceae). Pacific Insects 22 (3-4): 217–236.
- Patterson, J.T. 1943 ("1942"). Studies in the genetics of *Drosophila* III. The Drosophilidae of the Southwest. University of Texas Publication 4313: 7–216.
- Patterson, J.T., and W.S. Stone. 1952. Evolution in the genus *Drosophila*. New York: MacMillan, 610 pp.
- Patterson, J.T., and R.P. Wagner. 1943. Geographical distribution of species of the genus *Drosophila* in the United States and Mexico. University of Texas Publications 4313: 217–281.
- Patterson, J.T., and M.R. Wheeler. 1942. Description of new species of the subgenera *Hirtodrosophila* and *Drosophila*. University of Texas Publications 4213: 67–100
- Robe, L.J., et al. 2014. Comparative ecological niche modeling and evolutionary ecology of Neotropical mycophagous Drosophilidae (Diptera) species. Studies on Neotropical Fauna and Environment, 49: 2, 79–94.
- Sabath, M.D., R.C. Richmond, and R.M. Torrella. 1973. Temperature-mediated seasonal color changes in

- *Drosophila putrida*. American Midland Naturalist 90: 509–512.
- Shorrocks, B., and P. Charlesworth. 1980. The distribution and abundance of the British fungal-breeding *Drosophila*. Ecological Entomology 5: 61–78.
- Shorrocks, B., and P. Charlesworth. 1982. A field study of the association between the stinkhorn *Phallus impudicus* Pers. and the British fungal-breeding *Drosophila*. Biological Journal of the Linnean Society 17: 307–318.
- Sidorenko, V.S. 1995. New data on Asian drosophilid flies (Diptera, Drosophilidae). Part I. Far Eastern Entomologist 8: 1–4.
- Stalker, H.D.m and W.P. Spencer. 1939. Four new species of *Drosophila*, with notes on the *funebris* group. Annals of the Entomological Society of America 32: 105–112.
- Sturtevant, A.H. 1916. Notes on North American Drosophilidae with descriptions of 23 new species. Annals of the Entomological Society of America 9 (4): 329–343.
- Sturtevant, A.H. 1918a. Acalypterae (Diptera) collected in Mobile County, Alabama. Journal of the New York Entomological Society 26 (1): 34–40.
- Sturtevant, A.H. 1918b. A synopsis of the Nearctic species of the genus *Drosophila* (sensu lato). Bulletin of the American Museum of Natural History 38 (14): 441–446.
- Sturtevant, A.H. 1921. The North American species of Drosophila. Washington, D.C.: Carnegie Institution of Washington, 150 pp.
- Toda, M.J., V.S. Sidorenko, H-a Watabe, S. Kholin, and N.N. Vinokurov. 1996. A revision of the Drosophilidae (Diptera) in East Siberia and Russian Far East:
 Taxonomy and biogeography. Zoological Science 13 (3): 455–477.

- Valer, F.B., E. Bernardi, M.F. Mendes, M.L. Blauth, and M.S. Gottschalk. 2016. Diversity and associations between Drosophilidae (Diptera) species and basidiomycetes in a Neotropical forest. Anais da Academia Brasileira de Ciências 88 (1) (Supplement): 705–718.
- Vilela, C.R., and G. Bächli. 1990. Taxonomic studies on Neotropical species of seven genera of Drosophilidae (Diptera). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 63 (Supplement): 1–332.
- Vilela, C.R., and G. Bächli. 2004. On the identities of nine Neotropical species of *Hirtodrosophila* (Diptera, Drosophilidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 77: 161–195.
- Wheeler, M.R. 1954. Taxonomic studies on American Drosophilidae. University of Texas Publications 5422: 47–64.
- Wheeler, M.R. 1963. Notes on the extant types of Dr. O. Duda's Costa Rican Drosophilidae (Diptera). Bulletin of the Brooklyn Entomological Society 58 (2/3): 51–61.
- Wheeler, M.R. 1981. The Drosophilidae: a taxonomic overview. *In* M. Ashburner, M., H.L. Carson, and J.N. Thompson (editors), The genetics and biology of *Drosophila*, vol. 3a: 1–97. London: Academic Press.
- Williston, S.W. 1896. On the Diptera of St. Vincent (West Indies) (Drosophilidae). Transactions of the Entomological Society of London 1896: 404– 417.
- Zhang, W., and X. Liang. 1995. Three new species of Drosophila (Drosophila) melanderi species-group in Hengduan Mountains of China (Diptera: Drosophilidae). Acta Entomologica Sinica 38 (4): 486–492. [in Chinese with English descriptions]

APPENDIX

Photomicrographs of Some Holotype Specimens and Labels

For images of the holotypes of *H. jaenikei* and *H. orbospiracula* see text figs. 7 and 9, respectively.

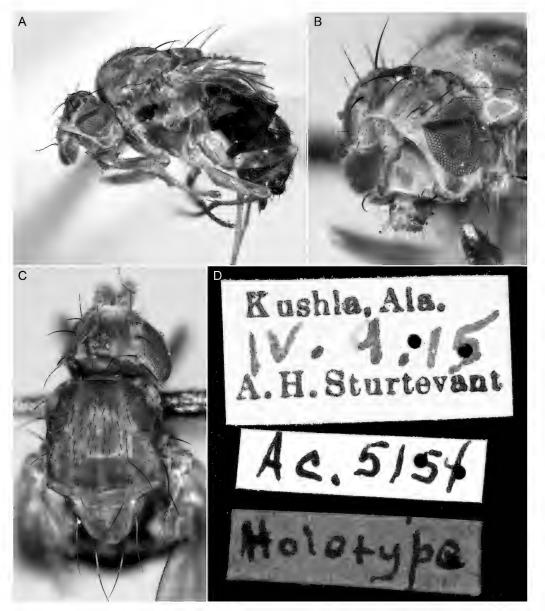


FIG. 39. *Hirtodrosophila alabamensis*, holotype female (AMNH). **A.** Habitus, lateral. **B.** Head, oblique frontal. **C.** Head and thorax, dorsal. **D.** Labels.

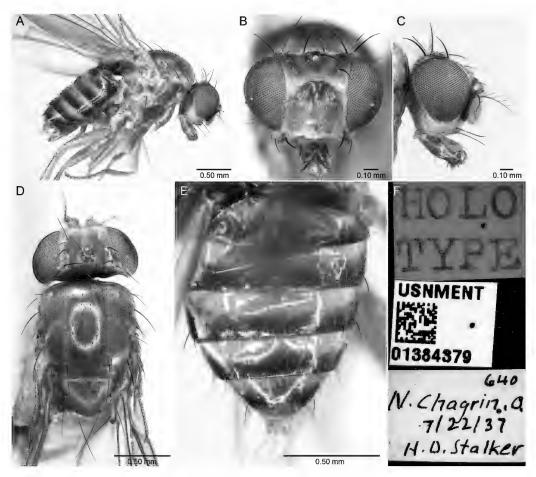


FIG. 40. *Hirtodrosophila chagrinensis*, holotype female (USNM). **A.** Habitus, lateral. **B.** Head, frontal. **C.** Head, lateral. **D.** Head and thorax, dorsal. **E.** Abdomen, dorsal. **F.** Labels.

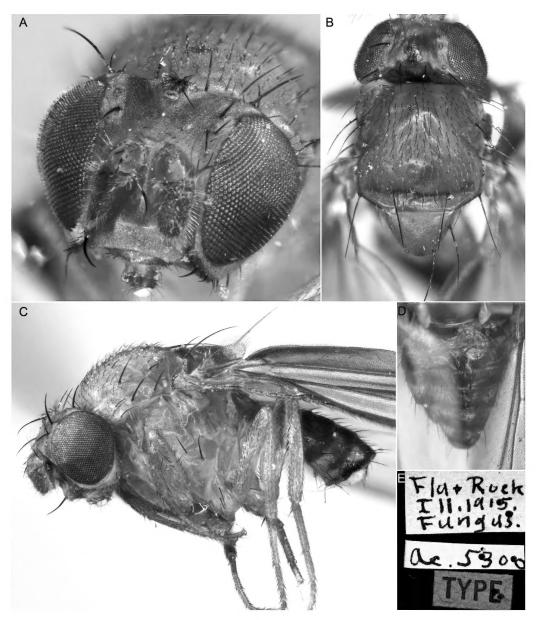


FIG. 41. *Hirtodrosophila duncani*, holotype female (AMNH) **A.** Head, oblique frontal. **B.** Head and thorax, dorsal. **C.** Habitus, lateral. **D.** Abdomen, dorsal. **E.** Labels.

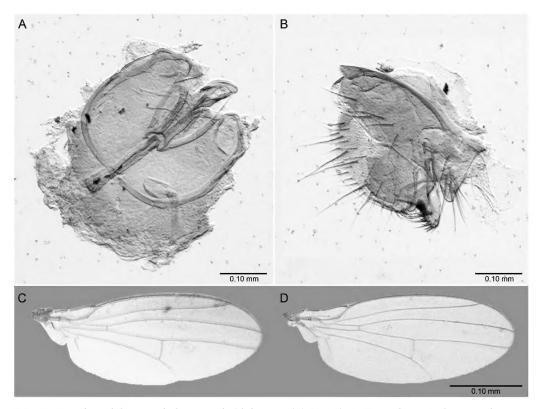


FIG. 42. *Hirtodrosophila grisea*, holotype male (slide mount) (AMNH). **A.** Hypandrium, aedeagus and associated structures. **B.** Epandrium and associated structures. **C, D.** Wings. No holotype specimen for *grisea* was found; this one matched the data of the type locality in the original description, so it was designated as the holotype.

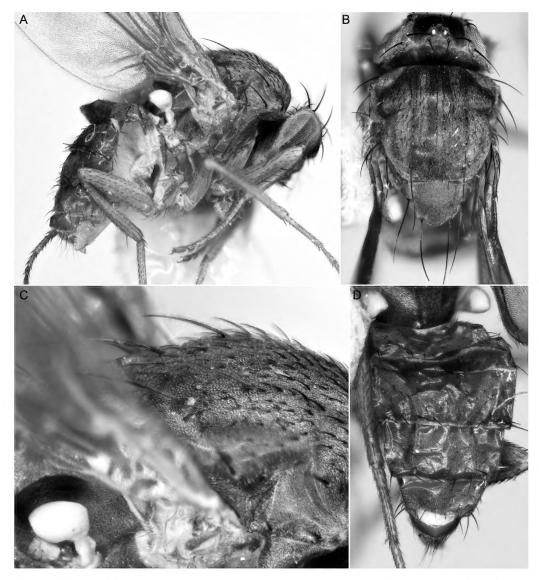


FIG. 43. *Hirtodrosophila grisea* (male, ordinary specimen), designated by Patterson and Wheeler (1942) as a paratype/allotype female of *H. longala* (AMNH). **A.** Habitus, lateral. **B.** Head and thorax, dorsal. **C.** Oblique view of notum, showing bluish pollinosity and enlarged acrostichals anterior to dorsocentrals. **D.** Abdomen, dorsal.

SCIENTIFIC PUBLICATIONS OF THE AMERICAN MUSEUM OF NATURAL HISTORY

AMERICAN MUSEUM NOVITATES
BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
ANTHROPOLOGICAL PAPERS OF THE AMERICAN MUSEUM OF NATURAL HISTORY

PUBLICATIONS COMMITTEE

ROBERT S. VOSS, CHAIR

BOARD OF EDITORS

JIN MENG, PALEONTOLOGY

LORENZO PRENDINI, INVERTEBRATE ZOOLOGY

ROBERT S. VOSS, VERTEBRATE ZOOLOGY

PETER M. WHITELEY, ANTHROPOLOGY

Managing Editor
Mary Knight

Submission procedures can be found at http://research.amnh.org/scipubs

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh. org/dspace). Order printed copies on the web from:

http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:

American Museum of Natural History—Scientific Publications Central Park West at 79th Street New York, NY 10024

⊗ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).

On the cover: Female of Hirtodrosophila Grisea (Patterson and Wheeler), from the southwestern U.S. and Northern Mexico.